

Modelling lactation in Pasture-based Dairy Cows Varying in Production Potential

by

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for the degree of Doctor of Philosophy**

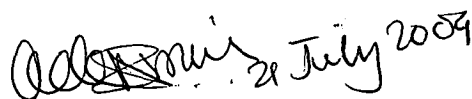


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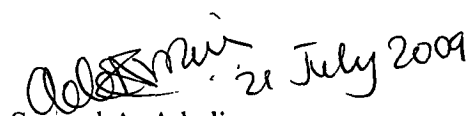
Preliminary

Declaration

This thesis contains no material which has been accepted for the award of other degree in any tertiary institution and to the best of my knowledge contains no material previously published or written by any other person, except where due reference is made in the text of this thesis


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List of Abbreviations

APR	Australia profit ranking
ASI	Australia selection index
BIC	Bayesian information criteria
BW	Body weight
BCS	Body condition Score
CF	Covariance Function
DIM	Day in milk
DMI	Dry matter intake
DMD	Dry matter digestibility
EBV	Estimated breeding value
EXP	Exponential
IG	Incomplete gamma model
HF	Holstein Friesian
HM	High merit
HTD	Herd test date
J	Jersey
FJ	Holstein Friesian x Jersey cross
LEG	Legendry polynomial
LM	Low merit
LQ	Log quadratic model
ME	Metabolisable energy
MID	Minimum day in milk
MSPE	Mean square prediction error
MXD	Maximum day in milk
NEB	Negative energy balance
NTD	Number of test-days
LCM	Lactation curve method
MLA	Meat and Livestock Australia
PR	Polynomial regression
RMS	Residual mean square

RMSE	Root mean square error
RRM	Random regression Model
SPL	Spline
h^2	Heritability
r_g	Genetic correlation
r_p	Phenotypic correlation
TDM	Test-day model

Abstract

The main objective of the thesis was to quantify the genetic and phenotypic determinants of variation in milk yield and composition, model the lactation pattern of pasture-based dairy cows varying in genetic potential for milk production and the comparative evaluation of empirical, mechanistic and random regression models as tools for management decisions. More than half a million lactation and pedigree data from Tasmanian dairy farms were sourced mainly from the TasHerd Milk Recording Organisation and the Elliott Research and Demonstration Station. The data were analysed using non-linear, generalised linear, mixed linear, multi-trait and random regression procedures in SAS and ASReml.

Initial and the incline to peak but not peak and total milk yield were significantly influenced by sire EBV choice. Early lactation milk yield potential was highly correlated with peak and total milk yield and could be used as *an early indicator of a cow's genetic merit*. Genetic (sire estimated breeding value (EBV) and cow production level in early lactation), physiological (age, parity and body weight), environmental (season and year of calving, lactation stage, nutrition and herd), factors influenced production traits. In addition days to first test-day post-partum, lactation length, number of test-days and their interactions affected curve shapes. Heritability of 305d milk, fat, protein and somatic cell counts were 0.41, 0.37, 0.32 and 0.28 respectively. Phenotypic correlations between milk and component yields ranged from -0.03 to 0.92, while genetic correlations ranged between 0.034 and 0.85.

Fourteen lactation functions including 8 empirical, 4 mechanistic and 2 semi-parametric types were fitted to test-day milk and milk composition yields. Empirical models adequately modeled the lactation of homogeneous group of cows but had varying error biases in fitting individual cow's profiles. Random regression, including cubic spline, models attained acceptable goodness of fit and permitted simultaneous evaluation of factors affecting curve shapes.

Significant contributions of the thesis to lactation modeling are the identification of suitable functions and the introduction of a new empirical model for pasture-based systems. High positive correlation between parameter c of this model with peak milk yield and lactation persistency suggests that it has the potential for future dairy genetic improvement. The knowledge of factors affecting curve shapes in pasture-based systems will be relevant in developing appropriate management strategies to mitigate early lactation production stress and maintain persistency.

Desirable as it is none of the tested mechanistic functions performed well. Suggestions for future work are; further research into the potential of existing mechanistic models to fit data across production systems and establishing a basis for understanding the physiological basis of empirical models. Lack of herd level management input inconsistent data recording pattern and incomplete test-date records were major obstacles of the study. Similarly, lack of economic indices made profitability modelling and overall farm economic analysis difficult. These constitute gaps in the current lactation data collation systems.

Chapter 1: Introduction

The post-parturient synthesis, secretion and evacuation of milk from the cow's udder in a physiological process controlled by nervous, hormonal and environmental factors is termed lactation. Milk secretion commences shortly after birth and due to increased mammary epithelial cell development, differentiation and involution, ascends to a peak 50-80 days post-partum, then declines gradually until it finally ceases due to apoptosis (death) of the cells (Capuco *et al.* 2001). This entire curvilinear cycle is known as the lactation profile whose shape and pattern can be modelled by mathematical functions and is controlled by genetic and environmental factors (see review by Beever *et al.* 1991, Swalve 2000, Jensen 2001 and Schaeffer 2004)

Test-day models are used in most countries to perform national genetic evaluations, estimation of shapes and changes in lactation curves as well as investigating sources of variation in dairy cattle populations. Although potentially useful, little attention has been given to the application of test-day models for management purposes (Caccamo *et al.* 2008). However, the potential of the test-day model for management use depends on its ability to describe within or between-herd variation that can be linked to specific management practices and adjust for such identified sources of variation. A wide search of published scientific literature reveals that very little or nothing is known about within- or between-herd variation attributable to genetic or phenotypic sources in Tasmania's dairy herds. This is a knowledge gap that has wide-ranging implications in pasture-based production systems. This thesis firstly hypothesises that *milk yield and composition are significantly influenced by breed, genetic potential, herd size, season and their second order interactions whose magnitudes will vary from one region to the other*. Answers from the testing of this hypothesis will provide significant foundational information on Tasmania's dairy production upon which further research questions could be built. Therefore, the first objective of this study was to evaluate the lactation performance of Tasmania's dairy herds and the influence of genetic and phenotypic factors determining milk yield and composition in grazing cows.

One of the main challenges of pasture-based dairying is the provision of adequate nutrition and management conditions to enable high merit cows attain their optimal milk production potential. Milk yield per cow has increased tremendously in the last three decades due to advances in genetics and improved management. Milk yield increased from 2000 to 5,500 kg/cow/lactation in herd-tested cows in Australia from 1930 to 1995 (ADHIS 2001). In order to continue to benefit from genetic gains, correct evaluation of the performance of high merit cows under diverse management conditions is essential. Statistical processing of phenotypic records makes it possible to partition production into genetic and environmental components thus facilitating the identification of superior individuals with desirable traits.

Decline in fertility of high merit dairy cows (Royal *et al.* 2000, Pryce *et al.* 2000) has led to the shift in emphasis of functional traits from milk yield per se to include reproductive traits. In Australia dairy farmers make informed choices on the best sires for mating their breeding cows on the basis of genetic potential or estimated breeding values (EBVs) of bulls utilising the Australian Selection Index (ASI). The inclusion of temperament, longevity and survival traits into the selection index in 2000 led to the development of the APR (Australian Profit Ranking) index. A key research question that remains largely unanswered is: What impact does the inclusion of temperament, longevity and survival traits in the sire selection index have on the lactation pattern of Tasmania's pasture-based cows that vary in genetic potential for milk production? What percentage of the variation can be explained by fitting an incomplete gamma function (Wood 1967, 1969) to the lactation profile of these cows? Wood's incomplete gamma function is the most commonly used empirical model to fit daily milk yield data, mainly because its three parameters can be related to biological components of the curve (Santos and Silvestre 2008, Dematawewa *et al.* 2007, Varona *et al.* 1998). The second hypothesis being tested in this study is that *initial milk yield and the rate of increase to peak are significantly influenced by index choice (ASI or APR) and Wood's incomplete gamma function will adequately model the lactation profile of pasture-based cows explaining over 90% of the observed variation irrespective of ASI or APR indices*. Therefore, the second objective of this study was to model the lactation pattern of pasture-based cows varying in genetic potential for milk production on the basis of ASI and APR using Wood's incomplete gamma function to test the goodness of fit between predicted and actual herd and individual cow milk yields.

Accurate knowledge of the lactation curve is essential for breeding (selection and culling), economic and management decisions, such as timing of supplementation, estimating total lactation yield from incomplete records (Wilmink 1987), early detection of metabolic diseases e.g. mastitis and sub-ruminal acidosis and forecasting herd or individual cow performance (Sauvant 1988). The models are also useful in genetic analysis of test-day records (Ptak and Schaeffer 1993, Guo and Swalve 1995) and to model the covariance between adjacent test-day records (Jamrozik and Schaeffer, 1997). Generally the purpose of modeling lactation is to predict, with minimum error, the average daily milk yield of animals, in the presence of various environmental factors. Lactation in pasture-based cows is unique because about 70% of the nutritional energy comes from pasture which is highly dependent on seasonal variation in climate and other production and pasture management practices. The response to these variations can influence the lactation pattern in individual or herd of cows more than in intensive or stall feeding systems (Tozer and Huffaker 1999, Val-Arreola et al. 2004). Consequently lactation functions may not be equally effective in fitting data from such a system.

The search for a robust mathematical model to describe the milk yield (MY) pattern of dairy cows has led to the development of several models varying in number of parameters and complexity (see review by Beever *et al.* 1991, Swalve 2000 and Jensen 2001). Lactation models may be empirical, when it relates input to output without considering the intervening metabolism, or mechanistic, when the model provides in addition explanation about the underlying physiological process. The suitability of a lactation model is determined by the accuracy with which it imitates the underlying biological process of lactation and adjusts for temporary environmental perturbations (Olori *et al.* 1999).

Wood's model is only one of many empirical functions used in modeling lactation. Val Arreola *et al.* (2004) fitted seven mathematical models to dairy cows managed under two management systems in Mexico while Silvestre *et al.* (2006) tested the accuracy of seven mathematical functions in modeling lactation in dairy cattle that were housed indoors and fed complete ration. Little has been published on modeling the lactation of Tasmania's dairy cows which are predominantly raised outdoors and fed on pastures. In an attempt fill this knowledge gap, answers to the following key research questions are essential: How

precise in predictive ability are the other empirical and mechanistic models in fitting the lactation profile of pasture-based cows? Is the prediction accuracy influenced by herd or individual cow data? The third hypothesis being tested in this study is that there are no significant differences in the goodness of fit of seven empirical, 5 mechanistic and two semi-parametric fitting test-day milk yield of homogenous groups and individual cow data, hence using any of them will be adequate in modeling the pattern of daily milk yield in Tasmania's pasture-based dairy cows. Furthermore, milk yield patterns of individual cows will be more varied and less accurately modelled than herd data. Therefore, the third objective of this study was to determine the goodness of fit of fourteen lactation models in a comparative analysis of their predictive characteristics in accurately fitting the lactation profile of pasture-based dairy cows in Tasmania.

The accuracy of lactation models reported in literature differs due to computation methods of the models (Tozer and Huffaker 1999, Landette Castillejos *et al.* 2000, Macciota *et al.* 2005), biological variation between individual cows (Olori *et al.* 1999), differences in management practices (Val-Arreola *et al.* 2004), environment variation including season and year of calving (Wood 1969, Goodall 1983, Lennox *et al.* 1992) and data sample properties (Berry *et al.* 2005 and Silvestre *et al.* 2006).

While the relevance and application of empirical and mechanistic models to the lactation profile of lactating cows is unquestionable, a constant draw-back of these models lies in serial correlations between test-day records and the inability of the models to simultaneously account for environmental factors affecting each test-day. Random regression models on the other hand, are now a popular choice for modeling traits that change gradually, continually with time and are measured repeatedly on individuals. The random regression mixed linear model was initially suggested by Henderson (1982), while Schaeffer and Dekkers (1994) suggested its use in analyzing test-day records where each test date is treated as a repeated measure of the same trait or as a separate trait. Recently, there has been an increasing number of research publications on the use of random regression models in dairy cattle (Mrode and Coffey 2008, Hammami *et al.* 2008), beef cattle (Sanchez *et al.* 2008, Aziz *et al.* 2005, Meyer 2004, Schaeffer 2004, Arango *et al.* 2004) and sheep (Molina *et al.* 2007, Fischer *et al.* 2004) for modeling test-day lactation or growth. To my knowledge, no such publication dealing with random regression modeling

has been reported in Tasmania's dairy industry, thus constituting a knowledge gap. Therefore this thesis tested a fourth hypothesis that *random regression models will improve the accuracy of lactation profile and identify factors that will aid management decisions in Tasmania's pasture-based dairy production systems*. The fourth objective of the study was to quantify the potential increase in the accuracy of modeling lactation profiles and accounting for factors affecting milk yield and composition through the implementation of a random regression model to estimate heritabilities and genetic and phenotypic correlations among lactation traits.

When pasture-based cows are supplemented (McEvoy *et al.* 2008, Rego *et al.* 2008, Flowers *et al.* 2008), associated responses in milk yield, liveweight and body condition score are normally expected. The questions needing answers in Tasmania's grazing dairy cows include: To what extent can the environmental and management factors be adequately partitioned without losing accuracy of lactation profile modelling? Are there substantial differences in the lactation patterns and phases between supplemented and non-supplemented grazing cows? The fifth hypothesis being tested is that *supplementing pasture-based dairy cows will lead to a partitioning of the extra energy into milk synthesis or liveweight and body condition thereby triggering diverse responses that can be accurately predicted by semi-parametric or test-day model*. Therefore, the fifth objective of this study was to quantify the effect of supplementation, liveweight and body condition score change on milk the yield profile in grazing cows and evaluate the predictive accuracy of a mathematical functions in describing the profiles of such interventions in lactating dairy cows.

In summary, the main aim of my thesis was to elucidate, for pasture-based cows, the predictive characteristics of the lactation profile and the associated genetic and phenotypic determinants. Specifically the objectives were:

- i) To evaluate the genetic and phenotypic sources of variation influencing Tasmania's pasture-based dairy production.
- ii) To test the goodness of fit between predicted and actual herd or individual lactation in cows of varying genetic potential (ASI or APR indices) using Wood's model.

- iii) To conduct a comparative analysis of the predictive characteristics and goodness of fit of fourteen lactation models fitted to daily milk yield and composition data of dairy cows.
- iv) To investigate the factors affecting lactation curve shapes and genetic evaluation of milk yield and composition through the implementation of a random regression model to estimate heritabilities and genetic and phenotypic correlations.
- v) To quantify the effect of supplementation, liveweight and body condition score in grazing cows on milk yield profiles and evaluate the predictive accuracy of semi-parametric functions in modeling their profiles.

Chapter 2: Literature Review

2.1 *Dairying in Australia*

The Australian dairy industry has ex-factory and farm-gate values of \$9.1 and \$3.2 billion respectively, with milk production concentrated mainly in the South-Eastern corner of Australia and the States of Victoria, Tasmania and South Australia accounting for 78% of the national milk output (Dairy Australia 2008). Victoria is the highest milk producing State (accounting for about 60% of the national milk output), Tasmania accounts for about 6% while New South Wales produces twice as much as Tasmania and South Australia.

Whereas milk sales constitute a vital component of the Australian dairy farmer's income, milk revenue has largely been driven by the international sales of dairy products since the deregulation of the production sector in 2000. Milk production continues to grow at an average rate of 3.5% except in 2000-2001 when widespread drought and high costs of feed grains resulted in production losses and subsequent reduction in farm sizes in many Australian States (Dairy Australia 2008). Industry statistics (ABARE 2008) showed that farm milk production in the 2007/08 season was 985,500L down from 1,044,470L in the previous season, although total farm receipts increased from '000 AUD 334,920 to 426,000 over the same period.

Pasture-based dairy production system

Dairy production in Tasmania, as in many other Australian States, is predominantly pasture-based. Three typical systems, based on the level of supplements used, described by Jesse (2006), include: *Miser Farms* which depend exclusively on grazing as their feed source; *Gap Feeders* use some supplemental feeds to balance seasonal variation in grass growth with supplementary feeds and *System Feeders* that use grain supplementation to boost per-cow productivity. In spite of system differences, fodder from pasture accounts for almost 60% of dairy cow feed in Australia. Purchased feed costs represented about 70 percent of total feed costs in 2002 (Dairy Australia, 2008) and nearly ninety percent of dairy farms use some form of concentrate, while hay and silage use per farm in 2002 was estimated at 150-170 tons (FAO 2007).

Year-round grazing is normal in Australia in contrast to intensive or stall feeding systems in the United States and parts of Europe. The use of intensive grazing presents challenges to dairy producers and nutritionists. This challenge is the provision of adequate nutrition and management conditions to enable high merit cows attain their optimal milk production potential. Insufficient energy is the major factor limiting milk production in Australia's pasture-based dairy industry (Kellaway and Harrington 2004). High milk energy demands in early lactation and insufficient dry matter intake as well as poor pasture quality during the summer and early autumn, corresponding to the months of December to February and March to May respectively, in the Southern Hemisphere, results in negative energy balance. Grazing cows therefore need well-targeted supplementary energy to attain their optimal potential for dry matter intake and milk production (Bargo *et al.* 2003). When used at different lactation stages, supplementation can potentially increase milk, protein and fat yields per hectare and per cow, lactation persistency, body condition score, and reduce input costs per litre of milk. However, supplemental feeding with pasture-based systems is more difficult to manage compared with confinement systems, due to less control of the forage component with a grazing system and consequent variability of daily nutrient intake. Similarly, milk yield/cow/day can be quite variable.

Milk yield per cow is often 1700 to 2800 kg/cow/year lower than that obtained with confinement systems (Jesse 2006). Grain supplementation also results in substitution and the rate of substitution increases with increasing pasture allowance (Bargo *et al.* 2003, Garcia and Fulkerson 2005). Therefore, optimising dry matter intake, maintaining high production, utilisation of home-grown feed, effective supplementation at least cost, good pasture management skills and maximising production per hectare without compromising individual cow yields are essential for successful pasture-based dairying. In addition, high pasture utilisation through high stocking rates is considered to be the key to the economic viability of pasture-based dairy systems (MacDonald *et al.* 2008, Chapman *et al.* 2004).

An appraisal of the lactation process and milk composition is necessary for understanding the complexities and interplay between the biological processes of mammogenesis, lactogenesis and apoptosis as they relate to the dairy cow's lactation curve.

2.2 The lactation process

Milk production involves the biochemical conversion of ingested nutrients into fat, protein and lactose and their secretion in milk. Lactation is initiated at parturition, either by suckling action or mechanical stimulation of the mammary gland. Three physiological processes controlled by hormones are implicated in the lactation process. These are mammary epithelial cells development, differentiation and involution (Knight and Peaker 1984, Imagawa *et al.* 1990). Lactation comprises of milk secretion and removal or ejection through suckling or the mechanical action of hand or machine milking. Cyclical structural changes in the population and function of epithelial cells in the udder of mammals, driven by hormonal and nervous changes, during and after pregnancy are central to the lactation process (Mephram 1987).

Milk yield and the shape of the lactation curve are determined by the number and activity per cell. The lactation cycle starts with *mammogenesis* or rapid cell proliferation during gestation, followed by cell differentiation or *lactogenesis* which, occurs just before parturition (Tucker, 1981, Capuco *et al.* 2001) and ends with cell involution (apoptosis) leading to cessation of milk yield (Knight and Peaker, 1984, Mephram 1987, Capuco *et al.* 2001).

Milk production starts at a relatively high level immediately after parturition, reaches a peak and then declines in response to the nutritional needs of the young animal. This pattern is also known as the *typical* lactation pattern in contrast to a continuously declining (*atypical*) production pattern which has been reported in some dairy cows (Olori *et al.* 1999, Macciotta *et al.* 2005), sheep (Cappio-Borlino *et al.* 1997) and deer (Landete-Castillejos and Gallego 2000). High peak and sharp post peak milk yield decline have been reported to be associated with metabolic stress and disease conditions (Collard *et al.* 2000, Terkeli *et al.* 2000) which in turn, have implications for the cow's milk yield and composition.

2.3 Milk and milk composition

Milk is a liquid, secreted by the mammary glands of female mammals to nourish their young. Milk is essentially an emulsion of fat and protein in water, along with dissolved sugar, minerals (including calcium and phosphorus), and vitamins, particularly vitamin B

complex (Kon 1972). In terms of composition, cow milk contains about 87.4 % water, 3-5.5% fat, 3-4% protein and other components such as carbohydrate, minerals and vitamins (Whittemore, 1980). Milk fat is the most variable component of milk, while milk protein and lactose are relatively more stable throughout lactation. Increasing global awareness of the health benefits of more protein-rich diets and the negative connotation for fat in foods have led to a shift in emphasis of milk payment systems around the world from milk yield *per se*, to milk and milk component yields (Lennox *et al.* 1992). For instance in May 1985, for the first time in Britain, the Milk Marketing Board price for milk protein exceeded that paid for fat contents, a clear indication of consumer preference (Lennox *et al.* 1992). Milk pricing system varies for different states in Australia. In Tasmania, a new milk payment system which came into effect in July 1990 puts the price of milk fat and milk protein at 2.22 and 3.64 Australian dollars respectively. This opens the opportunity for interested dairy producers to identify cows with potential for high milk protein yields and the adoption of management practices that promote high milk protein content and improve economic returns.

2.3.1 Milk fat

Milk fat is a complex mixture of lipids known as triacylglycerols containing three fatty acids covalently bound to a glycerol molecule by ester bonds. Fat content pattern is inversely correlated with milk yield, i.e. milk fat declines from the beginning of lactation, reaches nadir and then rises gradually towards the end of lactation. Milk fat is the major source of lipid for building adipose tissue and energy reserves during gestation. Negative energy balance in early lactation is a major issue in high producing cows. In order to meet milk energy demands and compensate for the shortfall in nutritional energy, high producing cows often mobilise large amounts of body reserves of fats, proteins, glucose and other nutrients leading to weight loss, milk fat depression and in extreme cases, metabolic diseases. Cows calving in good body condition have higher percent milk fat than cows that enter lactation in thin condition (Stockdale 2000). Milk fat depression is usually manifested when fat and protein yields fall between 2.5-3% and below 3%, respectively, in poorly conditioned cows or when well-conditioned cows produce milk fat content of 0.9-2.5% with higher protein values accompanied by depressed dry matter intake at any lactation stage (Sharma *et al.* 1990).

2.3.2 *Milk protein*

The primary group of milk proteins are the caseins and whey proteins including enzymes, hormones, growth factors and other proteins. The major milk proteins apart from caseins include β -lactoglobulin and α -lactalbumin. They are synthesised in the mammary epithelial cells and are unique to the mammary gland (Mephram 1982). Milk protein percentage is positively correlated with milk fat percentage. (Hurley 2003). Under conditions of NEB, the catabolism of proteins can lead to excess production of ketone bodies and development of fatty liver (Eicher *et al.* 1999). The relationship between fat and protein levels and the level of milk urea nitrogen are currently used as an indication of whether cows are consuming adequate quantity of energy and protein in their diets or not, as well as to assess the potential likelihood of developing metabolic stress in cows (Jonker *et al.* 1998, Eicher *et al.* 1999).

2.3.3 *Lactose*

Lactose, the major carbohydrate in the milk of most species, is a disaccharide composed of the monosaccharides D-glucose and D-galactose, joined in a β -1, 4-glycosidic linkage. Lactose plays a major role in milk synthesis (Mephram 1982). Lactose content is the least variable component of milk (Davies *et al.* 1983). Cows are at risk of ketosis in early lactation because of the rapid drain of blood glucose accompanied by an underlying condition of negative energy balance. All cows are at least borderline ketotic, but only 4-12% develop clinical symptoms.

2.3.4 *Water, minerals, vitamins and other components*

The primary function of milk is the provision of nutrients for building the skeletal and soft tissues of the young animal. Calcium and phosphorous are the major minerals found in milk and both play important roles in bone and skeletal formation. Other elements in milk include potassium, magnesium, sodium, chlorine and other trace minerals mostly found in association with micelles, casein, milk fat and enzymes. Minerals contribute to the buffering capacity of milk, the maintenance of milk pH, the ionic strength of milk, and milk's osmotic pressure (Mephram 1982). Milk also contains vitamins for various physiological functions. The fat soluble vitamins, A, D, E, and K, are found primarily in the milk fat while the B vitamins are found in the aqueous phase of milk.

Milk contains leukocyte cells, known as somatic cells in cow milk. There are several types of milk leukocytes including macrophages, lymphocytes, neutrophils, and eosinophils. Milk also contains some sloughed off epithelial cells from the teat's inner linings, the ducts, and the alveoli. The concentration of leukocytes in milk varies with the species, infection status of the gland, and stage of lactation. Other components of milk are bioactive factors such as hormones and growth factors, enzymes, cellular proteins, and others (Mephram 1987). Milk yield and composition is influenced by a myriad of factors that are genetic, physiological, environmental and management-dependent.

2.4 Factors affecting milk and milk component yields

The production of the lactating cow is determined by genetic and non-genetic factors. These include breed, age, parity, sire merit, production potential, hormones, lactation stage, age and body weight at calving, gestation, length of the dry period, seasonal effects, disease occurrence and plane of nutrition (Danell 1982). Animal nutritional requirement is conditioned by physiological status, nutrient content and digestibility of available feeds, palatability, gut fill and endocrine factors. The three main phases of lactation believed to have genetic components are initial, peak and post-peak persistency milk yields (Ali and Schaeffer 1987). Generally, higher milk yields at the early stages of lactation are accompanied by low constituent percentages (Sharma *et al.* 1990). Maintenance of high post-peak milk production level (persistency) depends on the number of secretory cells lost, the extent of cell replacement and the retention of synthetic capacity by each cell (Wilde and Knight, 1989).

Circulating levels of systemic hormones, such as prolactin, insulin and adrenal steroids, influence the rate of mammary cell secretion. Mammary cell activity and milk production react to endocrine manipulation (i.e. treatment with bovine somatotropin) and to increasing the frequency of milking during the declining phase of lactation. The combination of enzymatic capacity per cell and cell numbers appear to explain the changes in milk production throughout lactation (Dijkstra *et al.* 1997). Energy is the most limiting nutrient in pasture-based dairy production (Kellaway and Harrington 2004). Although pasture is the cheapest energy source, high-merit cows need additional energy supplements to meet milk energy demand.

2.4.1 Genetic factors

Breed

Dairy cattle are broadly categorised into two types; *Bos taurus* (European) and *Bos indicus* (Zebu). Together, they account for 90% of global milk production (Mephram 1987). The main dairy breeds in Australia are the Holstein-Friesian, Jersey, Guernsey, Brown Swiss and Ayrshire. These breeds vary in size, body conformation, milk, protein and fat yields. The choice of cattle breed depends on factors such as climate, production system, and available land for grazing and other production objectives. Table 2.1 shows the mean milk, fat and protein yields of dairy cows in Australia. The table shows that there were observable breed differences in milk fat percentage with Jersey cows clearly at the top (4.89%) compared with other commercial dairy breeds with the lowest values (3.81%). Similarly, in terms of milk yield, the Holstein-Friesians produced significantly ($P < 0.05$) more milk than the rest of the breed. Milk yield did not differ between the Illawara, Australian Red and the Brown Swiss breeds. However, there were no obvious significant differences in protein percentage among cow breeds but the Jersey, Guernsey, Ayrshire and the Dairy shorthorn breeds produce significantly lower total protein than the rest of the breeds. The small number of cows reported in some of the breeds might be responsible for the higher production figures compared to the more commercial breeds. Milk composition varies within breeds and among individual cows. Generally, milk protein percentage is positively correlated with milk fat percentage. Jensen (1995) investigated the influence of cattle breed on milk composition and reported that the percentages of milk fat were 4.1, 4.0, 5.0, 3.5, 5.5, 4.9 for Ayrshire, Brown Swiss, Guernsey, Holstein, Jersey and Zebu, respectively, while percentage protein and lactose for the same breeds were; 3.6, 3.6, 3.8, 3.1, 3.9, 3.9 and 4.7, 5.0, 4.9, 4.9, 4.9, 5.1 respectively.

Table 2.1 Variation in average dairy cow lactation performance of some dairy breed in Australia.
Category Production averages*

Breed	Number of Cows	Milk (L)	Fat%	Fat (kg)	Protein %	Protein (kg)	Lactation Length (d)
Holstein	498,302	6,418	3.88	249	3.25	209	314
Jersey	73,888	4,638	4.89	227	3.76	175	302
Holstein/Jersey Cross	94,645	5,401	4.37	236	3.48	188	299
Guernsey	31,662	5,003	4.33	217	3.51	175	316
Ayrshire	2,517	4,980	4.11	205	3.37	168	309
Dairy Shorthorn	4,499	4,283	4.14	177	3.65	156	293
Illawarra	362	5,431	4.05	220	3.49	190	307
Unknown Breed	7,368	5,606	3.99	224	3.31	185	304
Australian Milking Zebu	25	5,130	4.02	206	3.41	175	322
Australian Red Breed	5,859	5,390	4.21	227	3.51	189	303
Brown Swiss	2,732	5,428	4.13	224	3.5	190	321
Aust Friesian Sahiwal	63	5,168	4.39	227	3.69	191	329
Total	721,922						
Average		5240	4.21	219.9	3.49	182.6	309.9

*Source: ADHIS (2005).

Genetic merit of Sires

Income from milk is the main source of revenue for dairy farmers, hence the interest in high-performing cows. Selection pressure on bulls is higher since most of the cows are needed to produce offspring for the next generation. Milk production cannot be measured on males, thus sire genetic evaluations must be based either on pedigree records of the females or on records of the progeny (progeny test). Van Vleck (1979) showed that evaluation on the basis of the progeny test has greater accuracy than pedigree evaluation. The genetic merit of the bull or the estimated breeding value (EBV), estimated from records of daughters and their contemporaries (MLA 2005), is an indicator of the genetic transmitting ability of a trait and is a very important tool for genetic decisions. The greater the genetic variance for a trait in relation to the total variance between individuals in the same or similar population, the higher the heritability of the trait and the better the prospects for genetic progress through selection.

Previous breeding objectives focused mainly on milk production traits (Miglior *et al.* 2005). However, interactions between strain and feeding system have been observed for milk production (Veerkamp *et al.* 1994; Fulkerson *et al.* 2001; Kolver *et al.* 2002; Kennedy *et al.*

2003), feed efficiency (Wang *et al.* 1992), body weight, body condition score (Berry *et al.* 2003) and fertility (Kolver *et al.* 2002). The realization that these other factors can impact farm profitability has led to a change of direction towards more balanced, profit-focused breeding objectives globally (Miglior *et al.* 2005).

Until 2000, the Australian Selection Index (ASI), based on production traits, was used as the index of choice for breeding sires. Industry demand led to the inclusion of longevity traits in an alternative index, the Australian Profit Ranking (APR). The aim of the APR is to maximise profit from genetic gain by predicting the profitability of a bull's progeny according to certain breeding objective (ADHIS 2001). Studies from New Zealand have shown that cows of high "genetic index" (high merit) at pasture produce more milk (20 to 40%), consume more herbage (5 to 20%), were more efficient converters of feed into milk (10 to 15%) than lower merit cows (Holmes, 1988). Similarly, Veerkamp *et al.* (1994) showed that increasing genetic index results in major increases in feed efficiency, reflecting increases in milk yield with cows fed indoors on silage/concentrate diets. In another study comparing high and medium genetic merit cows for milk yields and reproductive traits, Snijders *et al.* (2001) reported that high genetic merit cows had higher milk production, incurred greater body condition loss between calving and first service than medium genetic merit cows. Furthermore, higher genetic merit cows had lower first and second service and overall conception rates and required more services per conception than the medium genetic merit cows. Peyraud and Delaby (2001) attributed the higher milk yield response (kg/kg grain) of 0.89, obtained in post-1990 experiments compared with 0.66 in pre-1990 trials, to increase in genetic merit of cows estimated at +0.1/kg concentrate every decade.

Precise estimates of genetic parameters are required for prediction of breeding values using appropriate statistical and genetic tools with large data sets. Advancement in micro-computer technology has made the estimation of breeding values on national datasets using multi-trait best linear unbiased prediction (BLUP) animal models and random regression models techniques computationally feasible, thus replacing sire models used in the past (Berry 2008).

Level of herd-cow genetic merit

The potential for genetic progress through selection is greater when there is high additive genetic variance between individuals in the population. In national genetic evaluation systems, variation in the performance of daughters of sires across herds is therefore an important tool for ranking sires. This variation can be quantified in terms of sire breeding index for the trait of interest or the production level of the cow, both of which can be influenced by environmental factors. Such factors are not always adequately recorded in test-day records. Heritability estimates will be biased if variances are assumed to be equal across herds (Boldman and Freeman 1990). However, logarithmic transformation of yields as a method of equalizing variances across herds alone may not effectively stabilize variances (Boldman and Freeman 1990).

Several studies in which variance components of milk yield were estimated from herds grouped by production level have indicated a positive relationship between production level and estimates of genetic and residual variances and heritability (De Veer and Van Vleck 1987, Dong and Mao 1988). Boldman and Freeman (1990) estimated additive genetic and environmental variances for all lactation milk yield and natural log of yield at three herd production levels by REML in a sire and nested-cow model and reported that variance components for untransformed yields increased with production level. Heritability was 0.18, 0.22, and 0.24 for untransformed yield in low, medium, and high producing herds.

Grouping by production level is also valuable in management decisions such as concentrate supplementation because there is experimental evidence showing that milk production responses to increasing levels of concentrate supplementation will be greater with higher yielding dairy cows (Delaby *et al.* 2001). In a study evaluating the response to concentrate in cows varying in genetic index, Shalloo *et al.* (2004) reported that the optimum system for cows with lower genetic potential for milk production is low level of concentrate supplementation, while that for cows with higher genetic potential for milk production is high level of concentrate supplementation. In addition to milk yield level in early lactation, the occurrence of *atypical* curve shapes is an artefact of some mathematical functions which do not have a rising phase (Tekerli *et al.* 2000, Macciotta *et al.* 2005). Thus, variation in yield pattern in early lactation is a basis for segregating cows on the

on the basis of production level. Furthermore, early lactation milk yield is an early indicator of cow genetic merit which can be a handy tool for genetic decision.

2.4.2 Physiological factors:

Hormones

Synthetic hormones such as oestrogen and progesterone have been used either singly or in combinations in various studies to induce cellular proliferation during gestation, but variability in response and histological abnormalities in mammary structure have precluded their universal use. Recent evidence suggests that optimal cell growth requires placental lactogen or growth hormone (GH). Injections of GH are effective in stimulating development of mammary parenchyma in heifers at puberty as well as in the nutrient partitioning in favour of milk production. Synthetic GH injected for 188 days increased peak yield and persistency in cows. Overall yield increase without change in composition was 36.2% compared with 16.5% obtained with natural GH extracted from bovine pituitary (Mepham 1987). The mechanism of change involved both partitioning of nutrients and increased food intake.

Capuco *et al.* (2001) showed that bovine somatotropin BST increased cellular proliferation in the mammary gland and that reduced energy balance adversely affected mammary cell proliferation. Bovine somatotropin administration increased the proportion of mammary epithelial cells expressing the nuclear proliferation antigen, Ki-67, from 0.5 to 1.6%. Increased persistency in mid lactation is attributable to increased rate of cell renewal in the lactating mammary gland. The prolactin-inhibiting drug bromocriptine when administered during the few days before and after parturition led to 38% increase milk yield in goats, although the physiological basis of the effect is yet to be fully explained. Synthetic oxytocin has also been used to stimulate milk let down in inhibited cows (Mepham 1987).

Stage of lactation

Milk yield and composition of milk vary considerably during lactation, with the major changes usually occurring soon after the start of lactation. Milk yield starts at a high level, reaches a peak and then declines. Fat and protein content are correlated, but inversely related to lactation yield (Groenewald and Viljoen, 2003). Milk yield in dairy cows is affected by lactation stage (Tekerli *et al.* 2000, Macciotta *et al.* 2005, Silvestre *et al.* 2005). Percentage

milk fat in colostrum ranges from 4.5% to 6.0% but drops to 3.5% - 5.5% depending on the breed after three days. On the other hand, percentage lactose increases slightly from 3.5 to stabilise at about 4-5 during the same period (Hurley 2003). Whittemore (1980) noted that colostrum contains twice the normal concentration of solids, five times the protein, approximately twice the fat and half the lactose. Fat and protein contents usually vary inversely to yield, while lactose declines steadily over the whole lactation period. Unlike fat content, there is little day-to-day variation in protein and lactose content of milk and any changes that occur are gradual.

Age and parity

Milk production increases with cow's age and parity due to increased body weight, larger capacity for dry matter intake, increase in size of the udder and recurrence of pregnancy and lactations (Capuco *et al.* 2001). Freeze and Richards (1992) reported that cows attained their maximum milk yield potential at an age of 6.5 years. Freeze and Richards (1992) also showed that whereas fat content increases with age, protein percentage depreciates as soon as the total milk yield starts to decline. On the contrary, Batra (1986) reported that cow's age did not significantly affect the lactation curve. First parity cows have lower lactation peaks but are generally more persistent than later parity cows due to energy partitioning towards maturity and mammary gland development. Age at first calving can influence not only the first, but later lactations as well. Mostert *et al.* (2001) found that during the first two parities, younger dairy cows have lower total milk yield.

Body condition and pregnancy

Prolonged selection for high milk yield has produced cows that readily mobilise body reserves in order to meet the energy requirement for lactation (Roche *et al.* 2006). Cows in good body condition at calving produce higher milk yield in the following lactation than cows in thin condition at calving (Stockdale 2000).

In seasonal calving pasture-based systems, cows are re-bred 50-60 days post partum. Oestrus and pregnancy depress milk yield during mid-lactation (Jamrozik and Schaeffer 1997). An increase in the level of circulating oestrogen and progesterone with advancing pregnancy inhibits milk secretion (Mephram 1987). Pregnancy does not appear to affect milk yield until the fifth month of lactation. In studies on the effect of stages of lactation

and pregnancy on milk and component yields, Sharma *et al.* (1990) reported that pregnancy stage accounted for small but significant variation in most traits in Holstein and Jersey breeds. However, the variation was greater in Holsteins, being 0.2 to 0.4% and <0.1 to 3.0% in yields and percentages of fat and protein and <0.1 to 0.2% and 0.1 to 1.1% for the same traits in Jerseys. Salama *et al.* (2005) also reported reduction in milk yield in goats due to pregnancy.

2.4.3 Environmental and management factors

Environmental factors that influence lactation are temperature, nutrition, season of calving, frequency of milking and diseases. Temperatures exceeding 25-29°C depress milk yield as well as lactose and protein contents due to reduction in dry matter intake. The deleterious effect of high temperature can be reduced through the provision of shade, cool showers and feeding of high density energy diets prior to the onset of the heat stress. Day length can also potentially reduce milk yield especially in temperate climates during winter when day length is significantly shorter. Provision of artificial lighting to increase daylight to 16 hours a day has been demonstrated to stimulate yield by 6-10% (Mephram 1987) through increased feed intake. There is also evidence that supplemental light increases the growth of mammary parenchyma in both pre-pubertal and post-pubertal heifers (Petitclerc *et al* 1985..

Nutrition

Over the years, different production systems have evolved in different countries due to differences in climate, access to and cost of land for grazing and technology. Whereas in many parts of Europe and America, cows are housed during the winter and the production system is intensive (i.e. there is greater proportion of compounded feed in the diet), production in Australia and New Zealand is still predominantly pasture-based (Jesse 2006). Grazing is limited by seasonality of grass growth and nutrient variability. Therefore, conserved forages in the form of silages, hay and high energy grains constitute important feed options. Physical form of presentation, frequency of feeding, particle size, energy density, availability of by-pass nutrients, substitution rate, cost and pasture allocation in relation to timing of lactation are all factors which can influence the usefulness of concentrate feed (Stockdale 2000). In an experiment comparing milk yields of cows feeding on high quality pasture and total mixed ration, milk yields were 29.6 and 44.1 kg/d,

respectively (Kolver and Muller 1998). The difference of 15 kg milk was attributed to energy losses for the pasture based cows in the form of dry matter intake (61%), energy for grazing and walking (24%), energy for extra urea excretion in pasture based cows (12%), energy for higher milk fat content from grazing cows (7%) and energy contributed from additional body weight loss from grazing cows (-4%) (Kellaway 1991, Dairy Farmers 2001).

Low dry matter intake of pasture has been identified as a major factor limiting milk production by high producing dairy cows (Bargo *et al.* 2003). Compared with pasture-only diets, increasing the amount of concentrate supplementation up to 10kg DM/day increased total dry matter intake by 24%, milk production by 22%, and milk protein percentage by 4%, but reduced milk fat percentage by 6% (Bargo *et al.* 2003). Milk production increased linearly as the amount of concentrate offered increased from 1.2 to 10 kg DM/day, with an overall milk response of 1 kg milk/kg concentrate.

Milking frequency

Older cows milked three times a day have been reported to produce 17% more milk per lactation than those milked twice per day without adverse effect on reproductive performance, but first parity cows milked three times daily gained less weight (Depeters *et al.* 1985). In goats, it has also been demonstrated that milking three times daily increased milk yield by 29% compared to twice daily milking. It was hypothesised that increased mammary growth might have been responsible because in one experiment, thrice-daily milked glands were heavier than controls (Mephram 1987). In another study, milking frequency significantly affected milk yield (+8% vs. -26%) for thrice- vs. once-daily milking. In addition, growth hormone (rbGH) treatment increased milk yield from thrice-daily milked udder-halves (+19%) and increased the size of mammary glands (Boutinaud *et al.* 2003). However, thrice daily milking has both physiological and management implications. One of the key factors of importance to future dairying in Australia is the availability and cost of labour. Increasing milking frequency is labour intensive. However, advances in micro-electronic systems and increased use of robotic milking machines will enhance multiple milking where cost is not limiting.

Season of calving and production

Milk yield and composition is also influenced by climatic conditions including season or month of calving and production system. Wood (1967) especially noted that the shape of the lactation profile is influenced by the calving season. Under pasture-based systems, a reduction in quantity and quality of pasture in the summer months (Southern Hemisphere) depresses milk yield. Similarly, cows calving in spring and winter produce more milk than autumn and summer calvers. This seasonal influence is thought to be mediated by the interaction of day light and ambient temperature. Batra (1986) reported that month of calving and lactation stage influenced lactation, while Jamrozik and Schaeffer (1997) showed the significant effects of days of year, age at calving and day in milk on milk yield.

Low temperature may increase the milk fat content, while high temperatures are usually associated with a decline in milk fat (Whittemore 1980). Heat stress is especially harmful to peak milk production. There is significant environmental influence on the expression of heritable traits in dairy cows. Production per cow varies between locations even under similar management practices. Herd location (Batra 1986), region and herd practices, day of the year (including weather conditions), month of calving, days in milk and medical treatments (Jamrozik and Schaeffer 1997) have been reported to have significant effects on test-day yields for Holstein dairy cows.

Diseases

Inadequate energy in early lactation involves the mobilisation of body nutrients including amino acids, fat, glucose, calcium, phosphate and water. This predisposes high merit cows to higher risks of metabolic stress such as acidosis, milk fever and mastitis as well as reproductive losses. Genetic selection for increased milk energy secretion in early lactation has produced cows that readily mobilise more body reserves (Roche *et al.* 2002), even to the detriment of the cow's health and fertility (Collard *et al.* 2000; Buckley *et al.* 2003). According to Eicher *et al.* (1999), an understanding of the relationship between fat and protein yield profiles and the levels of urea nitrogen in the milk, also known as milk urea nitrogen, are useful aids in determining the level of metabolic stress in the dairy cow.

2.5 Why model lactation?

The shape of the lactation curve has been a subject of interest to animal scientists over the decades because of its importance for farm profitability, management and animal health

decisions. Milk is the main source of income for the dairy enterprises, but the profitability of the dairy enterprise is also influenced by factors such as milk quality (in terms of percentage of solids and freedom from contaminants like somatic cells), genetic merits and herd health status and other factors all of which can influence milk yield at various lactation stages. For decades, the pattern of the lactation profile has been used as an index of the performance of the dairy cow or herd. Accurate knowledge of the lactation curves is therefore relevant to management and research of dairy production systems such as timing of supplementation, estimating total lactation yield from incomplete records and forecasting herd performance on monthly or individual cow basis (Sauvant, 1988). From a management point of view, therefore, the knowledge of the lactation profile of lactating dairy animals is required for feeding, breeding and economic management of a typical dairy herd.

Dairy cows vary in their response to supplementary feeds due to genetic and physiological factors. Buckley *et al.* (2000) and Roche *et al.* (2006) reported that high merit cows produce more milk per kilogram of concentrate feeds than low merit cows. Knowing when the cow will attain peak yield can be used to plan supplementation to meet the animal's nutritional requirement during various stages of lactation, reduce cost, and possibly maintain peak yield for as long as possible (Tozer and Huffaker 1999). Milk energy demand is greatest in early lactation and dry matter intake is inadequate to meet the lactating cow's energy needs, leading to the negative energy balance phenomenon. Supplementation helps to counteract the deleterious effect arising from body reserve mobilization and potentially leading to fat infiltration and ketosis.

Lactation curves are also useful for the identification of individual animals. Although most animals have the *typical* lactation profile, the incidence of *atypical* lactation or continuously declining curves, may range between 25% (Rekik and Ben Gara 2004) to 30% (Olori *et al.* 1999, Ramirez-Valverde *et al.* 1998). Identification of animals with a relatively constant yield throughout lactation will help in targeting supplementation while those exhibiting high peak yields followed by sudden decline might be exposed to the risk of physiological stress (Tekerli *et al.* 2000). Such information is vital in the identification of sick animals before the manifestation of clinical symptoms and in identifying animals with special dietary needs (Gipson and Grossman, 1989).

Information provided by lactation curves also assist in making culling decisions and milking strategies (Sherchand, *et al.* 1995). For instance, it may not be worthwhile to carry on milking an animal for an extended period of time if it yields most of its milk early in lactation and then shows a sudden decline thereafter. Fitting lactation curves to milk components can also reveal cows with high fat to protein ratio, which is not desirable in a healthy herd (Mephram 1987). Lactations that follow a flatter curve may, however, result in a slight reduction in total milk yield (Varona *et al.* 1998).

Lactation models are essentially predictive and the objective is to predict yield on each day of lactation with minimum error in the presence of environmental perturbations, in order to determine the underlying biological pattern of milk yield. The extent of the usefulness of a lactation model depends on how well it succeeds in imitating the biological lactation process and how well it adjusts for environmental and other factors that could influence production (Olori *et al.* 1999). Profiles can therefore be used to predict individual animal or herd future milk yields.

The use of milk quotas to meet market needs for liquid milk and dairy products can help the dairy enterprise in making decisions about herd composition for meeting production goals. Animals in a dairy herd that peak at a lower, but more sustainable level of yield (i.e. animals that produce milk at a greater level of persistency) may be more desirable than those with high but short peaks (Ferris *et al.* 1985). It is possible for dairy enterprises to use the lactation profile to identify cows with suitable production patterns to achieve herd peak milk yield when liquid milk can attract the best price (Lombaard 2006). The study of lactation curves is also relevant for studies of seasonality in milk supply for processors, as having such results makes it possible to assess the impact of any change in calving pattern and its subsequent effect on the seasonal pattern of milk supply (Quinn *et al.* 2003).

Dairy management in pasture-based systems is targeted at taking advantage of the pasture growing season to increase pasture utilisation and milk yield per hectare. In such systems, calving seasons are often synchronized; thus, the availability of fluid milk can be seasonal, with periods of glut and scarcity. In a deregulated system such as in Australia, it is important that farmers get the best economic value for their milk and milk products. The knowledge of the lactation profile of the herd can be used to plan production and milk sale. Lactation profiles are also important in the beef industry. The milk yield of the dam is the

single most influential factor in the weaning weight of a beef calf (Kim *et al.* 1998). The knowledge of the lactation profile of the beef cow would impact on developing the best feeding and weaning strategies for farm economic efficiency.

Fitting a parametric curve to the lactation profile generates parameter estimates which have genetic components and can be useful in estimating breeding values (Jamrozik and Schaeffer 1997, Swalve 2000, Schaeffer 2004). Traditional breeding value estimation was based on 305-d cumulative milk yield. However, improvement in micro-computer technology has facilitated the use of daily milk or test-day yields, thus increasing the accuracy of genetic estimation. Nevertheless, the knowledge of the lactation profile for management purposes must be used with caution. Whittemore (1980) warns that the use of lactation curves in both research and farm can only be a guide to monitor performance on the basis of herd pattern, so that deviations can be easily detected, causes identified and corrected.

2.6 Lactation models

Functions that describe change over time are of interest because they help us to understand or explain how biological traits change over time and how to manipulate such changes for improved productivity. The mathematical modelling of milk production usually concerns measures of time taken at different intervals during lactation. In the classical approach, a mathematical function of time is fitted to milk production as

$$y_t = f(t) + e$$

where $f(t)$ is continuous and differentiable in the whole interval of time that corresponds to the lactation length and e is the random residual (SAS. 2004). Through estimating the variance components of the parameters defining a typical function, the regular function underlying lactation can be dissociated from environmental perturbations or random noise. They are also used to separate curves of homogenous groups of animals and to make predictions about test-date records. Lactation models vary in complexity, the number of parameters estimated and the functionality in terms of explaining the underlying biological process of lactation (Beever *et al.* 1991). Although the mathematical form of various lactation models are described in Chapter 3, the three parameters of the incomplete gamma (IG) model (Wood 1967) is described below because references have been made to these parameters throughout this chapter.

2.6.1 Empirical models of lactation

The IG function (Wood 1967) is the most often used function to model lactation in dairy cows mainly because a technical meaning can be assigned to its three parameters (SAS 2004). The model has the form

$$y_t = at^b \exp(-ct)$$

where y_t is the average milk production at time t , a is scaling factor which represent yield at the beginning of lactation; b and c are factors associated with the incline leading to peak yield and the post-peak yield decline slopes of the lactation curve respectively. The IG model has been used to estimate the lactation curves for Holstein-Friesian cows in the United Kingdom (Olori *et al.* 1999, Canada, Freeze and Richards 1992), the USA (Scott *et al.* 1996), Mexico (Val Arreola *et al.* 2004) and Australia; (Tozer and Huffaker 1999).

Criticisms of the IG model include overestimating initial and late lactation milk yield and underestimating yields in mid-lactation (Scott *et al.* 1996). In addition, the persistency measures of the IG model are difficult to interpret biologically (Grossman *et al.* 1999). Another criticism of the IG model is that production level is zero at time 0, which is untrue in most mammal species. However, other authors such as Tozer and Huffaker (1999) justified the IG model by suggesting that the initial milk yield, colostrum, is of little economic significance and would normally be excluded from the lactation data. Rowland *et al.* (1982) argued that the Wood persistency measure is dimensionless and can be a valuable measure in comparing persistency of lactation within individual cows at different parities and among individual cows within a herd.

The polynomial regression (PR) model (Ali and Schaeffer 1987) has been fitted as a functional lactation model (Olori *et al.* 1999), and as a sub-model in RRM (Jamrozik and Schaeffer 1997, Kettunen *et al.* 2000). Although achieving very good convergence compared with other models (Ali and Schaeffer 1987, Olori *et al.* 1999, Silvestre *et al.* 2006), the model has been criticised as being over parameterised and having high correlations among parameters (Kettunen *et al.* 2000).

Although the diphasic model (Grossman and Koops 1988) gave a good fit to lactation data, criticisms remain that no biological justification exists to view lactation as a multiphasic process (Rook *et al.* 1993). The incidence of double peak lactation has been attributed to improved yield when cows are turned to pasture (Goodall 1986, Lennox *et al.* 1992, Garcia and Holmes 2001) and to illness or sub-clinical health problems in cows (Scott *et al.* 1996).

2.6.2 Mechanistic models of lactation

A general limitation of most empirical models is that the fitted parameters do not lend themselves to direct physiological interpretation and yield estimates sometimes fall beyond the range of biological significance (Neal and Thornley 1983, Dijkstra *et al.* 1997, SAS. 2004). In addition, milk yield during early lactation is overpredicted, peak milk production is underpredicted (Rowlands *et al.* 1982, Grossman and Koops 1988), residuals are autocorrelated (Goodall and Sprevak 1984, Grossman and Koops 1988), and model parameters are highly correlated, suggesting an over-parameterised model (Dhana 1981).

A mechanistic model which related milk synthesis to the underlying biological process was proposed by Neal and Thornley (1983). The model was fitted to data from a 44-week lactation to generate curves in reasonable agreement to *typical* lactation shape with residual sum of squares of 0.048 (kg/d)^2 . According to Dijkstra *et al.* (1997) the practical use of the model is limited because the inputs that are required are not generally available. Major criticisms of mechanistic models are the number of parameters and varying degrees of goodness of fit to monthly TD records (Dijkstra *et al.* 1997, Pollot 2000, and Val Arreola *et al.* 2004).

The advantage of mechanistic models over empirical models are that they do not pre-determine the shape of the lactation curve but rather fit curves based on the response to various inputs (Beever *et al.* 1991). They are useful in modelling short term responses of tissues to environmental stimuli, such as feed intake (Black *et al.* 1981).

2.6.3 Test-day random regression models

Parametric models, although useful in estimating average lactation curves of homogeneous groups of animals, are limited by their *a priori* assumption of curve shapes, problems of data connectedness (SAS 2004), inability to simultaneously account for the influence of

temporary environmental effects known to affect lactation, and covariances between adjacent TD records. Test-day models are free of these limitations and are also useful in mixed models for estimating variance components for genetic analysis and improved management (Swalve 1998).

Test-day milk yields of lactation recorded at different ages represent a case of *repeated measures*, in which measurements are taken in sequence over time on the same animal. Test-day milk yields are correlated, dates with test-days close in time being more correlated than dates farther apart in healthy cows under stable management. In addition, there are covariances among adjacent test-dates due to genetic variation and other short term environmental effects such as feed quality, intake, disease, and estrus (Ali and Schaeffer, 1987, Wade *et al.* 1993, Carvalheira *et al.* 1998). These patterns of correlation and covariances can produce complicated structures among test-dates that, if ignored, may result in inefficient analysis or incorrect conclusions. The general notation of random regression models (RRM) and the terms in the model are described in Chapter 3.

There has been an increasing number of research publications on the use of RRM mixed models in dairy cattle in the last few years (Mrode and Coffey 2008, Hammami *et al.* 2008), beef cattle (Arango *et al.* 2004, Meyer 2004, Aziz *et al.* 2005, Schaeffer 2004, Sanchez *et al.* 2008) and sheep (Fischer *et al.* 2004, Molina *et al.* 2007) for modelling TD lactation or growth. The energy balances in early lactation of dairy cows were predicted using simulation models (e.g. De Vries and Veerkamp 2000) and regression equations (e.g. Heuer *et al.* 2000). Such models are also relevant for cross-country genetic evaluation of sires although such evaluations are more difficult to model. In addition, genetic evaluations using TD records lead to large volumes of data for more precise genetic evaluations.

The advantages of mixed models over fixed regression methods include: 1) better handling of hierarchical structures in the lactation data, 2) the ability to deal with connectedness arising from unbalanced or sparse data, 3) variable amounts of information from different lactations can be used, 4) lactation curves can be corrected for the effects of main environmental factors, 5) avoidance of the use of extended records for culled cows and for records in progress (Swalve 2000), 6) the potential of reducing milk recording cost by using different recording schemes, 7) the use of early predictors of genetic merit for selection decisions (Nicholas and Smith 1983, Swalve 2000), and 8) the possibility of more

precise genetic evaluation from multiple records per cow instead of one 305d record (Ptak and Schaeffer 1993, Swalve 1998). Major disadvantages are that the volume of data to be analysed is much larger and the models used will tend to have many more parameters to be estimated compared with the traditional models for aggregated lactation yields (Swalve 2000, Schaeffer 2004).

Test-day models evaluation methods

Test-day data can be analysed as a split-plot in time design with the animal as the main plot and the different time intervals as sub-plots, or as components in RRM. The RRM often includes a herd test-date (HTD) effect, previously defined as a herd-year-season effect lactation model, a random animal or genetic effect, one or more permanent environment effects and a residual term. Fixed regressions are used for the curvilinear pattern of the production in the course of the lactation to account for similarities of lactation curves within specified groups of animals (e.g. regions, parity and age classes), while the animal genetic effect can be modelled as random regressions with a covariance structure among the regression coefficients. (Schaeffer and Dekkers 1994). Environmental factors affecting each TD such as, lactation stage, milking frequency, age at calving and days pregnant are modelled by nesting the sub model for DIM within the fixed effects (Ptak and Schaeffer 1993). Modelling the herd effect as HTD instead of herd-year-season of calving reduced residual variances (Swalve 1995, Pösö *et al.* 1996, Strabel and Szwaczkowski, 1997).

Test-day models have also been treated as multiple-trait models under which TD records within and between lactation are considered as separate traits (Reents *et al.* 1995a and Reents *et al.* 1995b). Swalve (2000) suggested that if genetic correlations among all considered traits are close to unity, a repeatability model such as a fixed regression model should be applied, while a multi-trait model will be more ideal if genetic correlations among traits (measurements) differ from unity. The multiple trait RRM has been applied to evaluate the effects of feed intake, body condition scores, and heart girth in dairy cows (Liu 1998, Jones *et al.* 1999, Gallo *et al.* 2001, Veerkamp *et al.* 2001).

Although multi-trait models are advantageous in having no assumed structures for the (co)variances among records taken at different DIM, difficulties arise in estimating the

fixed effects and the dispersion parameters pertaining to the additive genetic and permanent environmental effects (Jensen 2001). Also, the multi-trait (co)variance components obtained does not allow a direct continuous description of the (co)variance structure (Gengler *et al.* 2001). Wiggans and Goddard (1997) proposed using canonical transformation to reduce the number of traits to fewer “pseudo traits” corresponding to the largest Eigen values of the covariance matrices for all the traits used in the model.

2.6.4 Semi-parametric models

Legendre polynomials

Legendre polynomials and cubic splines represent a form of semi-parametric function suggested for lactation modelling (Kirkpatrick *et al.* 1990, White *et al.* 1999). Orthogonal polynomials are infinite sequences of real polynomials $P_0, P_1, P_2 \dots$ of one variable x , in which each P_n has degree n , and such that any two different polynomials in the sequence are orthogonal to each other. They can be incorporated into random mixed regression models to account for curve shapes and other fixed effects. Silvestre *et al.* (2006) and Bohmanova *et al.* (2008) compared many models including RRM with Legendre polynomials and linear splines and demonstrated that models with splines had the best overall performance based on goodness of fit measured by the lowest percentages of squared bias, highest correlations between predicted and observed records and lowest residual variances.

Ptak *et al.* (2004) evaluated milk yield data of Holstein-Friesian cows of diverse genetic composition using second, third and fourth order Legendre (LEG2, LEG3 and LEG4) polynomials and reported mean daily milk yield (kg/d) of 17.1 ± 5.15 which peaked at 21.5 kg on day 34 of lactation. Mean daily yield (kg) of fat and protein were 0.71 (SD=0.24) and 0.55 (SD=0.18) respectively. Peak yields were 0.95kg at DIM 9 and 0.70 kg at DIM 6, respectively. Protein yield peaked about 4 weeks before the maximum milk yield was attained. Variation between daily milk yields was lowest in early lactation whereas variation between fat yields was greatest during the same period. LEG of even orders produced more accurate predictions of 305-d yields for all traits. It was concluded that odd order LEG may be inappropriate for modeling lactation curves that vary from the standard (Ptak *et al.* 2004).

Cubic Splines

Various authors have described the relevance and application of splines to TD lactation data of dairy cows. Jensen (2001) described spline models applied to TD data as a class of test-day models while Swalve (2000), Huisman *et al.* (2002), and Guo and Schaeffer (2002) classified the spline model as a random regression test-day model with a spline function as a sub model of the lactation curve.

Verbyla *et al.* (1997) suggested using splines for fitting growth curves. Woolliams and Waddington (1998) used splines to model lactation curves at the phenotypic level and reported a two-fold increase in precision relative to the use of the IG model. White *et al.* (1999) used cubic splines to model TD milk yield data and showed that splines are capable of picking up features of the lactation curve that are missed by the random regression model. Meyer (2005) used cubic polynomials to analyse the data of Angus cattle and reported that cubic polynomials were more likely to yield erratically high estimates of variances at the highest ages.

2.6.5 The search for the master model

Models are derived from hypotheses and data; therefore, their versatility depends on the ability to simulate reality and adapt to changes in inputs from which they were developed. They also reveal gaps in knowledge which makes them sometimes fall short of representing reality (Beever *et al.* 1991). The suitability of different models reported in the literature has been diverse, for instance, Olori *et al.* (1999) reported that the PR model gave the best fit in a farm-based study, while Garcia and Holmes (2001) found no difference in average lactation predicted by both diphasic and linear-based split-plot models. Papajcsik and Bodero (1988) evaluated twenty lactation models and concluded that the IG model and its derivative gave equally good fits for cows in a sub-tropical environment. In comparison, Val-Arreola *et al.* (2004) fitted five models to data from small scale and intensive systems in Mexico and found that the mechanistic model presented by Dijkstra *et al.* (1997) was best. Consequently no single model has emerged as fitting all lactation scenarios.

Macciotta *et al.* (2005) compared the mathematical relationships of several lactation curves and concluded that comparisons among parameter values and (co)variances, rather than goodness of fit, could yield more robust, reliable, and easy to interpret results if performed

within groups based on curve shape. On the other hand, Olori *et al.* (1999), in a study using Friesian cows in Ireland observed that differences in goodness of fit of models are due to biological variation in individual cows rather than the mathematical form of the model. Papajcsik and Boderó (1988) compared six models and reported that the IG model and its derivative in which the decline function was replaced by a hyperbolic cosine function were found to be the best representations of the lactation curve for the data on Holstein cows that they used.

Although achieving better fits with lactation data, the main disadvantage of semi-parametric models according to Ptak *et al.* (2004) is that their parameters have no biological meaning. Despite the better fits obtained from the more complex models, simpler empirical models tend to be preferred by many researchers (Tozer and Huffaker 1999). This thesis contributes to the knowledge of lactation curve modelling and their suitability for dairy management decisions in Chapter 6 by evaluating the goodness of fit of empirical, mechanistic and semi-parametric models to lactation data from pasture-based dairy systems.

2.7 Models describing milk components yield

The current milk payment system is an incentive to produce milk of higher milk constituents. Fitting of lactation curves to milk constituents is therefore as important as fits to milk yield. The knowledge of the milk solids profile of individual cows can help farmers in constituting herds that best meet the production target markets for specialized production and attract a premium price for dairy products. Both milk fat and protein are often modelled with the same functions that are used to model milk yield, on the condition that they are able to take on a convex form. Lactose, on the other hand, requires a function that has the ability to model decline, as no rise to peak is present. Very little work has been done on modelling the lactose content of milk (Lombaards 2006).

Wood *et al.* (1980) suggested that the IG model could equally be applied to model changes in live weight, feed intake, milk cell counts and yields of milk constituents. Goodall (1986) fitted a seasonally adjusted IG model to milk and fat percentages while Wilmink (1987) fitted the EXP model to milk fat and protein yields. Other attempts at fitting lactation curves to component yields are by Morant and Gnanasakthy (1989), De Boer *et al.* (1989), who fitted fat yields to a diphasic function, and Sakul and Boylan (1992). In addition to fat

and protein yields, Morant and Gnanasakthy (1989) and Sakul and Boylan (1992) also fitted curves to lactose yields. The IG model provided a satisfactory fit with respect to the fat and protein content of milk, but was unable to adequately model the proportion of lactose contained in milk. Mostert *et al.* (2001) and Groenewald and Viljoen (2003) fitted milk and fat yields to the reduced EXP and the IG models respectively. In this thesis, four lactation models were fitted to milk and component yields (see Chapter 7).

2.8 Body weight, body condition score and lactation

Although body weight and milk yield can be quantitatively measured in animals, body condition is measured subjectively. Body weight varies between animal breeds, body size and age of dairy cows and it is also influenced by degree of fatness and gut fill (Enevoldsen and Kristensen, 1997), which are dependent on the pregnancy and lactation stages (Koenen *et al.* 1999). The BW profile of dairy cattle usually follow a characteristic pattern, i.e. a sharp fall in BW at parturition coinciding with the expulsion of the fetus and uterine contents; followed by a decline due to the catabolism of body reserves to supply energy for milk production (Jones *et al.* 1999, Koenen *et al.* 1999). Then there is a subsequent rise until the next parturition.

The body condition score is a quick, non-invasive and inexpensive means of estimating fat stores in dairy cows independent of the animal's frame size and BW (Waltner *et al.* 1993). It has long been demonstrated as a valuable tool in predicting the productive and reproductive performance in many domesticated animals (Wildman *et al.* 1982, Butler and Smith 1989, Domecq *et al.* 1997a, 1997b). Body condition score can be influenced by production year (Gallo *et al.* 1996), feeding level (Mao *et al.* 2004), milk production system (Washburn *et al.* 2002), parity (Gallo *et al.* 1996, Mao *et al.* 2004), and the genetic makeup of the animal (Berry *et al.* 2002, Roche *et al.* 2006).

Many studies have demonstrated the interrelationship between body weight (BW), body condition score (BCS) and production in farm animals (Wildman *et al.* 1982, Domecq *et al.* 1997a, 1997b, Roche *et al.* 2006). The decline in fertility and metabolic stress in high merit cows, deriving from negative energy balance in early lactation, is attributed to previous aggressive breeding strategies focusing on milk production *per se* to the exclusion of other traits (Miglior *et al.* 2005). This breeding strategy has resulted in a cow that readily

mobilizes condition to support lactation (homeorhesis): (Bauman and Currie, 1980, Roche *et al.* 2006), only regaining lost condition when energy surplus to milk production, maintenance, and pregnancy is satisfied. Roche *et al.* (2006) depicted the relationship between BCS and milk production as mirror images of the lactation profile. Energy stores are therefore a key component of milk production.

Body weight and BCS change during lactation in response to the efficiency of the cow in partitioning of nutrients between milk yield and BW gain. The variation in BW throughout lactation may be due to the genetic association between BCS and BW and the patterns of tissue mobilization, which differ throughout the lactation (Berry *et al.* 2002). Waltner *et al.* (1993) and Domezq *et al.* (1997b) demonstrated the importance of the changes in both BW and BCS during lactation in deriving correlations with milk yield.

2.9 Fitting curves to body weight and body condition scores

The relationship between body weight (BW) and body condition score (BCS) is important in understanding the production efficiency of the dairy cow and is useful in management and nutritional decisions. Production efficiency of a lactating cow refers to her ability to partition energy intake as effectively and efficiently as possible into milk production (Mao *et al.* 2004). Keown and Everett (1986), Gallo *et al.* (1996), and Pryce *et al.* (2002) argued that BW and BCS would provide a better biological explanation of differences in milk synthesis capacity of dairy cows varying in maturity than age at calving.

High producing dairy cows are unable to meet their milk energy requirement in early lactation due to limitation in energy intake resulting in negative energy balance (NEB), body reserve mobilisation, body weight loss and metabolic stress (Van Arendonk *et al.* 1991, Berry *et al.* 2002). This stress may impact upon the reproduction and immune systems leading to fertility and health problems during and beyond the NEB period (Collard *et al.* 2000). Similarly, high merit cows have a tendency to lose more live weight in early lactation and gain less live weight from nadir to end of lactation (Horan *et al.* 2005).

Broster *et al.* (1969) reported a negative relationship between BW change and milk yield at 126 days post-partum. Wood *et al.* (1980) represented the curves of milk yield and BW of

several breeds of British dairy cows over twenty weeks in a lactation period using the IG model. Similarly, Korver *et al.* (1985) constructed a function incorporating live weight level (scale), together with variables representing pregnancy status and reported the maximum decline in liveweight during early lactation. Berglund and Danell (1987) and Lopez-Villalobos *et al.* (2001) used the Wood's model (Wood *et al.* 1980) to predict liveweight in their respective studies and reported that the model fitted the data with an R^2 value of 0.67.

Quinn *et al.* (2006) modelled liveweight data of Irish dairy cows and reported that of the three models tested; Wood (1980), Wilmink (1987) and Guo and Swalve (1995), the latter had the lowest MSPE value although it had problems of multi-collinearity. They concluded that liveweight changes of a dairy cow could be modelled as a function of age, lactation and pregnancy. Mechanistic models were used to predict feed intake from milk yield and body weight (Monteiro 1972, Wood 1976, Williams *et al.* 1989) and vice versa (Bruce *et al.* 1984). Chumei *et al.* (2006) applied the IG model to fit milk yield, metabolisable energy intake and body weight profile of Holstein cows in Japan.

Garnsworthy (1988) and Grainger *et al.* (1982) used data from DMI and weight gains to estimate the relationship between BW and BCS of Holstein cows and concluded that because the energy density of pasture in Australia is unlikely to exceed 11.5MJ ME/kg DM, it is better to have cows calving at BCS of 4.5-5.4. They reported depressed DMI with increased incidence of metabolic diseases at BCS>6, while cows with lower BCS gave lower milk yields due to the partition of energy towards body condition (Kellaway and Harrington 2004). There is a need to further elucidate the interrelationship of milk production, feed intake and body weight changes in early lactation under pasture-based systems. This need is addressed in Chapter 8 of this thesis.

2.10 Lactation and reproduction

Milk yield, fertility and health are the most important traits that influence profitability of dairy production. The genetic correlation between fertility and milk production traits is generally established to be antagonistic (Castillo- Juarez *et al.* 2000), mainly attributed to the coinciding of peak production with the on-set of oestrous and the prevalence of metabolic disease such as mastitis (Haile-Mariam *et al.* 2003). Lactation involves great

metabolic investment in the accumulation of body reserves of lipids and proteins during gestation in order to meet the energy demand of lactation. Tamminga (2000) argued that the excessive mobilization of body reserves in early lactation due to insufficient lactation energy predispose high genetic merit cows to metabolic stress and reproductive problems.

Suriyasathaporn *et al.* (1998) reported that cows calving at BCS<3 (scale 1-5) had lower first-insemination risks. In their study, BCS loss between calving and 45 days post calving was associated with increased day's open and days-to-first insemination. Cows with body condition scores <2 after Day 45 and before first insemination were less likely to be inseminated and become pregnant compared with cows that had a higher body condition (Suriyasathaporn *et al.* 1998).

Infertility in dairy cattle causes considerable losses in the dairy industry. Genetic improvement in milk yield has been implicated in the reduced fertility of high merit cows. Evidence in the literature suggests that high merit cows are particularly susceptible to the problem of poor conception rate and non-pregnancy to first service. Pregnancy rates in cows declined by 0.45% per annum in the United States from 1975 to 1997 (Butler and Smith 1989, Beam and Butler 1999), while calving rate to first service in the United Kingdom declined at a derived average of 1.0% per annum over the same period. Calving rate to first service of a typical herd was approximately 40% (Darwash *et al.* 1999, Royal *et al.* 2000).

Genetic parameters for BCS have been reported by several authors (Veerkamp 1998, Jones *et al.* 1999, Dechow *et al.* 2001, Koenen *et al.* 2001). Cows genetically inclined to have higher BCS during the lactation are reported to have fewer days to first service, fewer services per conception and a shorter calving interval than cows that are genetically thin (Pryce *et al.* 2000, 2001, Dechow *et al.* 2001). The genetic correlation between energy balance and first luteal activity was reported to be moderately negative after adjustment for yield (Veerkamp *et al.* 2001). Negative energy balance in early lactation due to high milk energy demand requires cows to mobilise body reserves in support of lactation. Negative energy balance and excessive body tissue mobilisation are associated with increased incidence of metabolic disorders and poor fertility (Baird 1982, Loeffler *et al.* 1999, de Vries and Veerkamp 2000).

Direct estimates of the heritability (h^2) of body condition score loss and the genetic relationship among condition loss, production and reproductive performance are limited. The change in h^2 of BCS from week 1 to week 10 of lactation was reported to be 0.09 in an experimental herd (Pryce *et al.* 2001). Additionally, genetic correlation estimates among BCS measured at various points during the lactation have been reported to be high, indicating that genetic variation for BCS loss may be limited (Dechow *et al.* 2001, Jones *et al.* 1999, Koenen *et al.* 2001). Body condition score loss from week 1 to week 10 of lactation was reported to be genetically correlated with higher yield, and extended days to first heat and calving interval in an experimental herd (Pryce *et al.* 2001).

2.11 Lactation profile and metabolic health

Lactation curve models deliver statistics that are useful in management, such as persistency of lactation, day of peak milk yield, as well as peak milk yield, and average curves for herds' production (Wilmink 1987, Schaeffer and Jamrozik 1996, Ptak *et al.* 2004). These statistics could be used to make within-herd comparisons, such as detecting test-day milk and component yields that are too high or too low compared with previous tests which may indicate the onset of metabolic disorders such as acidosis or udder diseases such as mastitis.

Deficiencies in energy balance and protein deficiency is reflected in the milk composition, especially milk fat and protein percentages. Although milk fat and protein percentages vary by breed, feed fibre content and levels of grains fed, ideal levels in early lactation for Holstein-Friesian cows are in the range 3.2-4.2 and 3.0-3.7%, respectively. As lactation progresses, the percentages drops to 3.3 and 2.9%, respectively, and then rises again throughout lactation to well above 3.7 and 3.4%, respectively. High percentages of fat and low milk yields indicate sickness or low feed intake, while low milk fat percentages could indicate rumen dysfunction, metabolic diseases or feed composition problems. Low protein percentages are indicative of energy deficiency.

Low milk fat can be classified into two categories: *milk fat depression* and *low fat test*. Milk fat depression is attributed to abnormal rumen function when there is excessive grains intake, high dietary fat levels, low nutrient detergent fibre (NDF) and or low effective NDF levels leading to a disproportionate partitioning of energy into weight gain and a higher percentage protein compared with fat. Low fat test on the other hand occurs when there is

ration imbalance and/or energy deficiency, resulting in low fat percentage, low peak milk yield, low dry matter intake and weight loss. Feeding high fibre diets result in higher levels of acetic acid, the main precursor of fat, in the rumen. Supplemental dietary fat and excessive body fat mobilisation, weight loss or gain can also change milk fat composition. Feeding low fibre or poor quality fibre, which is not being eaten, is another cause of low milk fat.

Excessively low or high fat % is therefore an alert signal or warning of potential serious health problems such as acidosis and laminitis. An abnormal fat to protein ratio is another good indicator of health or metabolic problems in the dairy cow. Fat: protein inversion (i.e., protein level equal to or greater than fat level) is indicative of improper rumen function and can be an early warning sign to intervene before major damage is done.

Low protein level in milk can be a concern for dairy producers not only because of reduced income from the current milk payment system but also because excessively low protein level (less than 3.0% for Holsteins) may indicate low protein in the ration or insufficient dietary energy. The relationship between milk protein percentage and the milk urea nitrogen (MUN) test is a good indicator of energy utilisation in dairy cows. Milk urea is related to the ratio between the energy available for microorganisms and degradable/soluble protein of the ration. Milk protein is limited mainly by the energy requirement of the ruminal biomass. Excess dietary energy is indicated when milk urea nitrogen is low (0.00-2.00 mmol/l) and milk protein percentage is high (3.5-4.5%). Optimum levels are within the range 2.5-5.0 (mmol/l) urea nitrogen and 3.2-4.5 % protein, respectively. High levels of both components would indicate an excess of crude protein in the diet.

The ability to handle lactation induced stress without becoming ill is extremely important, from both an animal welfare and economic perspective (Wood *et al.* 2003). An understanding of the lactation profile for milk and constituent yields over lactation may provide insight into the incidence of metabolic conditions and provide information about genetic factors associated with metabolic stress which can be used in selection decisions. The incidence of metabolic and reproductive disorders that originate from the physiological stress of high milk yield would be lower for cows with flatter lactation curves (Madsen 1975, Pradhan and Dave 1973, Rao and Sundaresan 1979, Sölkner and

Fuchs 1987, Tekerli *et al.* 2000). This thesis also aims to evaluate the test-day milk constituent data of pasture-based dairy cows to establish herd production pattern which can be a basis for comparing constituent profiles for different herds and individual cows in the study area.

2.12 Persistency of lactation

Persistency is defined as the ability of the dairy cow to maintain high level production after attaining peak yield. Total milk yield depends on peak yield and persistency. There are many definitions of persistency (reviewed by Gengler 1996, Jakobsen 2000). However, it is often regarded as the flatness of the lactation curve and should be independent of lactation stage. Persistency is calculated as the month's milk yield divided by the preceding month's yield expressed as a percentage. On average, the persistency should be about 94-96% (i.e. milk yield in each month is about 95% of the previous month's yield). After peak production, milk yield of heifers will drop 0.2% per day while milk yield of mature cows will drop about 0.3% per day. Wood (1967) in the IG model defined lactation persistency as the negative power of (the incline rate plus unity) the decline rate while Pollott and Gootwine (2000) defined it as the rate of loss of milk secretion midway between peak and end of lactation.

A flatter lactation at a given production level is preferred because it would permit the use of cheaper feed (i.e., roughage) around peak yield (Sölkner and Fuchs 1987) and a reduction in stress due to high peak production (Zimmerman and Sommer 1973 as reported by Jensen 2001). Jakobsen (2000) confirmed the usefulness of a simple measure of persistency based on production decline from DIM 60-280 as proposed in the Canadian test-dat model (TDM) (Schaeffer *et al.* 2000).

Jakobsen (2000) also investigated the genetic relationship between persistency and disease resistance in dairy cattle and supported the hypothesis proposed by Zimmerman and Sommer (1973) that flatter lactations are less prone to high disease risks. She used records of production and disease incidence, defined as total number of veterinary treatments for any disease, from ca. 8000 primiparous Danish Holstein cows and found a genetic correlation between persistency and disease resistance in the range 0.20- 0.50. Information on persistency would especially be useful in situations in which disease resistance cannot be measured directly due to lack of large-scale recording programs, and therefore the

actual economic value of persistency may well depend on local conditions and production systems (Jensen 2001).

Evidence in the literature of genetic evaluation suggests that h^2 is greatest during mid lactation and that correlation between adjacent test-dates in mid lactation are higher and close to unity. Consequently, it may not be very useful to consider all individual test-dates jointly in a multiple trait evaluation despite its obvious advantages, in view of the inherent problems of large covariance matrices (Swalve 1998).

2.13 Factors affecting the shape of lactation curve

Income from milk is the main source of revenue for dairy farmers. In a deregulated system such as in Australia, milk price is determined by world market. Therefore, dairy producers have to adopt more efficient production practices that meet not only the demand for fluid milk but also high milk constituents as required by dairy manufacturing industries. Regardless of the pricing system for milk yield, economic efficiency of the dairy farm depends on attainment of high production levels and maintenance of persistency at minimum costs. An abrupt decline in milk yield after the peak increases production costs because yield will be distributed less equally over the complete lactation (Gengler 1996). These production measures are influenced by both genetic and non-genetic factors.

Differences in the shape of the lactation curve are often expressed as differences in the magnitude and sign of the decline phase or post peak yield. Consequently, lactation curves are classified as *typical* or *atypical* based on production pattern. Explanations for the occurrence of declining curve types are not consistent. While Olori *et al* 1999 attributed it to genetic differences among individual cows; Rook *et al.* (1993) observed that secretory cell population might already be in a declining phase at parturition.

Essentially the same factors affecting total milk and constituent yield also affect the production pattern throughout lactation. Production of milk and milk components varies with stage of lactation or DIM (Grossman and Koops 1988, Wood 1967). Milk production and composition also differ among dairy cow breeds (Madgwick and Goddard 1989), individual cows (Olori *et al.* 1999), genetic merit (Horan *et al.* 2005, Roche *et al.* 2006), parity, calving season, nutrition, pregnancy (Olori *et al.* 1999, Tozer and Huffaker 1999,

Tekerli *et al.* 2000), production environment (Val-Arreola *et al.* 2004, Roche *et al.* 2006), management practice and production systems (Garcia and Holmes 2001).

2.13.1 Genetic factors

Differences in the pattern of milk and constituent yield over the entire lactation phase have been reported by many authors. Rekik and Ben Gara (2004) observed that high producing cows with *typical* curves tended to have the highest peak milk yield and consequently the highest 305-d yield (Tekerli *et al.* 2000). Irrespective of herd type, Friesian cows exhibiting the *typical* curve shapes had higher initial, peak and total milk yields compared with those showing the *atypical* curve shapes. However, Gipson and Grossman (1989) did not observe an effect of breed on the shape of the lactation curve.

Variation in individual cow curve shape has been reported by many authors (Macciotta *et al.* 2005, Olori *et al.* 1999, Pérochon *et al.* 1996). Between 20-30% of cows show the *atypical* lactation curve types, i.e. curves without the characteristic lactation peak (Macciotta *et al.* 2005, Olori *et al.* 1999, Rekik and Ben Gara, 2004). These differences are attributed to genetic make up and genetic x environment interaction effects resulting in different expressions of genetic merit.

2.13.2 Physiological factors

Parity

Lactation curves in first parity cows have lower peaks and greater persistency. Wood (1970) noted that parity and season of calving were the dominant factors with the greatest influence on the lactation curve and suggested their inclusion in a model for more accurate prediction. Second parity cows attained earlier peak yields than first parity cows (Rowlands *et al.* 1982). Hansen *et al.* (2006) reported breed and parity effects on curve parameters. Similar results were reported for dairy goats by Gipson and Grossman (1989), who found that initial yield, peak yield and total yield were lower in first parity than in third parity does.

Rekik and Ben-Gara (2004) applied the incomplete *gamna* model (Wood 1967) to test-day lactation of Tunisian Hosltein–Friesian cows and reported that first parity cows had the lowest initial, rate of decline, peak and total milk yields but had the highest lactation

persistence, while third parity cows had the highest initial, peak and total milk yields. In the same study, the initial milk yields of cows with *typical* lactations were 13.89 ± 7.4 , 17.46 ± 9.0 , 19.56 ± 9.9 and 17.86 ± 9.8 for parity 1...4 cows, respectively. The corresponding values for cows showing the *atypical* curve shapes were 48 ± 57 , 166 ± 2312 , 63 ± 49 , and 78 ± 128 . In cows with *typical* curve shapes, the incline phase of the curve averaged 0.26 ± 0.2 and 0.23 ± 0.2 for first and third parity cows respectively, while the decline rate and peak milk yields averaged 3.63 ± 2.0 , 5.08 ± 2.4 and, 26.49 ± 5.7 , 32.45 ± 7.6 for first and fourth parity cows respectively. Milk yield (kg) at 305-d was higher in cows with *typical* lactations and ranged from 6735 to 7591 compared with 6088 to 6857 in cows showing the *atypical* curve type. Similarly in cows with *atypical* curve, parameters *b* and *c* of the incomplete *gamma* model ranged from -0.14 ± 0.2 to -0.17 ± 0.2 and 0.16 ± 1.7 to 1.12 ± 1.8 respectively.

Another potential effect of parity on curve shapes was reported in the study of Val Arreola *et al.* (2004). Their comparison of five models showed that the mechanistic model of Dijkstra, always gave the lowest Bayesian information criterion (BIC) indicating the best fit for first parity cows. The other models only marginally improved on the fits of the Gaines (Gaines 1927) and Wood IG model in the other parities. They attributed this difference to the absence of well defined peaks in first parity cows. However, Rekik *et al.* (2004), and Macciotta *et al.* (2006) noted the possible influence of data size and structure on the results.

Parity also influenced the different parts of the lactation curve. Val Arreola *et al.* (2004) reported that the incline phase was always statistically significant and was higher for cows in intensive systems than for those in small-scale systems. Furthermore, primiparous cows had a lower slope in the incline phase than second and third-parity cows. According to the authors, other features of the milk production curve were ambivalent; the intermediate phase increasing with parity for the empirical models while the rate of decline phase indicated that later parity cows have a less persistent lactation than primiparous cows.

Portolano *et al.* (1996) in their study of the lactation of Comisana sheep observed a positive correlation between parity and peak yield, while parity and time of peak yield were negatively correlated. Akpa *et al.* (2001) reporting on the performance of Maradi (Red Sokoto) goats found that herds, season of parturition and parity affected the shape of

the lactation curve. Peak milk yield increased with increasing parity up till the third or fourth parity and time of peak yield was later for first than for later parity does (Groenewald and Viljoen 2003). Similar results have been reported on lactation in dairy goats (Kala and Prakash, 1990, Rabasco *et al.* 1993, Kominakis *et al.* 2000).

Macciotta *et al.* (2006) showed that age at calving in water buffaloes had a significant effect ($p=0.05$) on the occurrence of standard or *typical* curves. In addition, when treated together, all curves for buffalo cows calving between 5 and 7 years seemed to have an *atypical* average shape, whereas all the other age classes showed standard patterns.

2.13.3 Environmental and management factors

Calving year, calving season, farm operation, and parity affect not only total milk yield but also the rate of milk production throughout the length of lactation, (Rekik and Ben Gara 2004).

Seasonal effect

Season of calving has significant effect on aspects of the lactation curve. Individual variation in cow milk production attributable to the animal (parity, pregnancy, or health) or the environment (calving season, management practices, and health) have been reported (Lennox *et al.* 1992, Sherchand *et al.* 1995, Pérochon *et al.* 1996). The highest initial milk yield (kg/d) of 16.83 ± 9.1 occurred in summer-calving cows compared with 16.44 ± 9.2 for cows calving in the autumn. The rise to peak yield was higher in autumn and winter calving cows being 0.25 ± 0.2 compared to 0.23 ± 0.2 for their counterparts calving in the other seasons. Persistency and peak milk yield ranged from 6.89 ± 0.08 to 6.87 ± 0.7 for autumn and summer calving cows and 30.39 ± 7.3 to 29.52 ± 6.9 for winter and summer calvers respectively (Rekik and Ben Gara 2004).

Season of calving and season of the year in which each observation occurred also contribute to the variance observed for daily milk production (Scott *et al.* 1996). Effects of season of calving might uniformly increase milk production throughout an entire lactation (Grossman *et al.* 1986, Wood 1967) and influence the shape of the lactation curve (Keown *et al.* 1986). Seasonal effects, such as spring lush pasture and heat stress in summer might also influence the shape of the lactation curve (Wood 1972). The length of the dry period

can influence milk yield at next calving. Milk yield is reduced if the dry period is less than 40-60 days while a longer dry period will prolong calving interval and decrease lifetime production of the cow.

Ferris *et al.* (1985) reported that season of parturition affected initial, peak, rise to peak, decline and the time of peak milk yield in dairy cows. In a study of Holstein-Friesian cows in Turkey, Tekerli *et al.* (2000) found that peak yield in dairy cows was higher when parturition occurred in autumn or winter while persistency was higher for cows that calved in summer and fall. Macciotta *et al.* (2005) observed that cows calving in summer showed a higher occurrence of *atypical* curves. In the case of dairy goats, Ruvuna *et al.* (1995) noted that does kidding in the hot dry season produced more milk than their counterparts kidding in the cold dry season. Gipson and Grossman (1990) confirmed that season of kidding in dairy goats affected both initial and peak yield.

According to Rekik and Ben Gara (2004) the odds of observing an *atypical* curve were different between herds and calving year, calving season, parity and days at first test-date. For instance, the probability of occurrence of *atypical* curves compared to that of *typical* curves increased by 36% and 45% in the spring and summer seasons, and by 20% in the second lactation, respectively. The probability of occurrence of *atypical* curves also changed by 6% with calving year and increased by 4% for each 1 day delay in the first test-day date. According to the authors the physiological basis of the increased chances of *atypical* lactation in second parity cows is not clear, but limited culling on low yield in the first lactation might be an explanation.

Herd or production system

Production system and other management factors had significant effects on various lactation curve traits (Tekerli *et al.* 2000, Rekik and Ben Gara 2004). Initial milk yield (kg/d) for Tunisian Holstein Friesian cows ranged from 13.58 ± 6.9 to 18.04 ± 9.6 for the different farming systems in cows showing *typical* lactation curves, while it ranged from 50 ± 114 to 146 ± 203 for herds showing the *atypical* curve types (Rekik and Ben Gara (2004). Similarly, peak milk yield and persistency ranged from 21.88 ± 5.4 to 33.00 ± 6.4 and 6.67 ± 0.7 to 7.08 ± 0.8 respectively. The rate of incline to peak ranged between 0.21 ± 0.2 and 0.26 ± 0.2 for cooperative and farmer herds while the decline rate ranged from 4.00 ± 2.1 to 4.57 ± 2.4 for farmer and state herds respectively. The rate of decline results contrast with

estimates 0.03 - 0.05 for the curve decline phase reported by Wood (1969) and Wood *et al.* (1980) for Friesians in the United Kingdom. The large standard deviations associated with the parameter estimates of Tunisian herds showing *atypical* curves shape suggest an important heterogeneity of the *atypical* curve.

Location

Tozer and Huffaker (1999) noted the main differences in the environmental conditions and management systems of dairying in the Northern Hemisphere and justified the fitting of lactation curves to production systems in the Southern Hemisphere using Australia as a case study. They evaluated five functional models with data from Australian dairy herds and reported that their results differ markedly from those earlier reported for Friesian cows in the Northern Hemisphere especially with respect to the magnitude of the parameters that determine the curvature of the lactation pattern and the slope of the declining phase after peak yield.

They reported initial milk yield (Kg/d) to be 21.99-30.31 in contrast to values in British Friesian cows as 34.12-52.98 (Wood 1969) and 32.7 (Wood *et al.* 1980). Tozer and Huffaker (1999) demonstrated that the size and time of peak lactation for cows in the Northern Hemisphere is much higher than for cows in New South Wales. Cows in the Northern Hemisphere had higher and later peak production compared to those in Australia. This is important for feed management in targeting supplementary feed and also for economic decisions (Kellaway and Porta 1993). Similarly, curve shapes may differ between systems, e.g. the lactation curve of stall-fed cows differs from that obtained from grazing systems (Garcia and Holmes 2001, Tozer and Huffaker 1999). However it can be argued that differences in the dairy management system or genotype x environment interaction can partly explain the results reported by the authors.

Nutrition and supplementation

Energy is the most limiting nutrient in the diet of pasture-based dairy cows and grain supplementation is often used to augment season induced nutrient shortage Stockdale (1999). Experiments measuring cow response to grain supplementation in Australia included short and long-term studies in early or mid to late lactation. Better milk yield responses were obtained when residual and cumulative responses in terms of post-supplementation milk yield and body weight gains were considered in addition to

immediate milk yield during long term studies. Responses were also better when pasture was restricted. Average immediate milk yield response of 0.6kg/kg supplement was reported (Robinson and Rogers 1983) under pasture restriction while no response or a negative response was obtained when pasture was fed to appetite (Hodge and Rogers 1984).

When residual responses of supplementation were monitored in long-term studies, Thomas *et al.* (1980) and Rogers and Robinson (1981) reported total responses over whole lactations of 2.5 and 1.1 kg/kg supplement respectively. On the other hand, Robinson and Rogers (1983) found no residual response when cows previously on restricted pastures were fed pasture ad-lib following supplementation. Similar results were reported by Hodge and Rogers (1984) and Dobos *et al.* (1987) when feeding pasture to appetite.

Wales *et al.* (2000) reported that their study did not substantiate the hypothesis of poor energy utilisation due to lack of fibre when cows grazing high quality irrigated pasture received barley as energy feed at 6.0 kg/day and grass hay at 0.5-3.0 kg. Cows grazing in the sole barley treatment maintained pasture intake while feeding of hay resulted in the substitution of hay for pasture. Milk production and composition were not improved by the feeding of hay. A similar conclusion was reached by Wales *et al.* (2001) when a cereal grain pellet was fed at 5.0 kg /day. Broster *et al.* (1969) reported marginal response to milk yield (kg) of 1.7, 1.5 and 0.8 milk per kg starch equivalent in early, mid and late lactations, respectively. A slightly lower response of 0.7 kg milk/kg concentrate (short term studies) and an extra 1.0 kg and 0.7 kg milk /kg supplementary grain and molasses (long term studies) was reported in experimental studies with cows grazing tropical pastures.

Sampling schemes

One of the factors influencing the shape of the lactation curve is lactation stage, especially DIM at first test-date (Rekik and Ben Gara 2004, Macciotta *et al.* 2004). Technology for automatic milk recording and availability of daily milk records facilitates the testing of the hypothesis of the influence of recording schemes on the goodness of fit of lactation curves. Silvestre *et al.* (2006) investigated the effect of test-date records based on four intervals from calving (8, 30, 60 and 90d) and two intervals between test-dates (4 and 8 wk) and confirmed the influence of sample properties on model performance.

In a study with restricted data, Ptak *et al.* (2004) used the second (L2), third (L3) and fourth (L4) Legendre polynomials to evaluate the lactation curves of Holstein-Friesian cows using lactation records restricted to 60, 100, and 200 DIM. The best fit and the most similar predictions of lactation yield for all traits were obtained using all available test-day records in the latter category. The differences between predicted yields were highest for records limited to 60 DIM. Estimates of protein yields varied most when the three forms of the Legendre polynomial were compared. Mean correlation coefficient between actual and predicted milk yield were 0.83, 0.88 and 0.94 when fourth order LEG was applied to production records limited to 60, 100 and 200Dim data respectively. The corresponding values for fat and protein were 0.81, 0.86, 0.90 and 0.81, 0.87, 0.93. However when applied to third order LEG, milk, fat and protein yields were 0.82, 0.84, 0.96 (60d), 0.72, 0.77, 0.92 (100d) and 0.28, 0.38, 0.54(200d) respectively. The authors further concluded that there was no practical difference between the 305-d yields calculated using data from the first 200 DIM (DF200) versus those calculated from the whole of the lactation data.

Schaeffer and Jamrozik (1996) compared two methods of 305-d lactation yield prediction, i.e. the use of standard lactation curves vs. the test interval method, and concluded that both methods yielded comparable estimates when the test-dates were regularly spaced. Correlation between predicted and actual 305-d yield ranged from 0.62-0.65 for one test to 0.99-1.00 for nine tests. They observed that generally correlation coefficients exceeded 0.90 when the prediction was based on at least four tests records per cow. Olori and Galesloot (1999) confirmed that the correlations between projected and official 305-d lactation yields increased with progressive length of the records when lactation records were calculated using projection factors derived on the basis of standard lactation curves. The correlation coefficients between official and predicted first lactation protein yields were 0.84, 0.89, 0.96 and 0.99 for lactations truncated at 50, 100, 200 and 300 DIM, respectively. Similarly, Wilmink (1987) reported that the correlations between predicted and realized 305-d milk yield increased from about 0.86 to 0.99 as the day of the last test progressed from the 50th to 210th day post partum.

Lactation functions

Differences in curve shapes arise from the presence or absence of an inflection point in the decreasing part of lactation (Druet *et al.* 2003, Macciotta *et al.* 2005), the mathematical function applied (Landete Castillejos and Galego 2000, Macciotta *et al.* 2005,), and/or

genetic differences in individual cows (Shanks *et al.* 1981, Olori *et al.* 1999). The number of parameters in a functional model has also been reported to influence the accuracy of prediction. Pérochon *et al.* (1996) reported that the models that predicted milk yield with uncorrelated residuals tended to be those with more than three parameters.

In a study of the relationship of the mathematical components of lactation functions, Macciotta *et al.* (2005) reported that while not discountenancing the role of biological effects, the occurrence of *atypical* curves is more a mathematical issue arising from the date at first test but also from the peculiar combinations of TD values and their distribution along the lactation length. These combinations determine the shape, *standard* or *atypical*, of the lactation curve. Wilmink's EXP model and Wood's IG model (see Chapter 3 for the equations of these models) classified approximately 18-36% of 17,000 lactations as *atypical*.

Tozer and Huffaker (1999) tested five lactation functions in pasture-based systems and reported that based on the asymptotic standard errors, all the other models except the IG had significant ($p < 0.01$) parameter estimates when fitted to data from first parity cows, Model performance for second parity cows was similar except that the monophasic function was almost a flat line and underestimated early lactation milk yield and none of its parameters was significant at any parity level. The Mitscherlich exponential models (Batra *et al.* 1986) did not converge with data from first and second parity Holstein-Friesian cows respectively. All the models represented fourth and later parity lactation fairly well, although the monophasic model (Grossman and Koops 1988) still underpredicted lactation by as much as 9-15L. Orthogonal polynomials and high parameter models such as the PR model (Ali and Schaeffer 1987) are capable of detecting different curve shapes based on the signs of the parameters.

2.14 Genetic Evaluation Methods

The genetic merit of the bull as measured by the estimated breeding values (EBVs) is a very important tool which has long been exploited to increase productivity of the dairy cow. EBV's are estimated as a functional index of trait transmission to the next generation and are calculated using measurements from live animals or combined with information from their pedigrees (MLA 2005).

In dairy systems with an annual calving pattern, lactation typically lasts for 270-305 days (Schaeffer and Jamrozik 1996). Therefore, genetic evaluations are traditionally based on 305-d milk yield in what is referred to as the routine method. However, for management and selection purposes it is sometimes necessary to predict 305-day milk yield from incomplete records or evaluate cows based on part records. The advantages of the latter are improvement in breeding value estimation from the use of a larger number of records and the evaluation of young cows, thus reducing generation interval. Advances in micro-computer technology and computation speed have facilitated genetic evaluation based on lactation curve test-day methods. Heritability estimates reported in literature vary depending on a number of factors including the type of estimation method (Olori and Galesloot 1999).

2.14.1 Fixed regression and lactation curve method

The one-step approach or fixed regression model was originally proposed by Meyer *et al.* (1987) in the form of a sire model, but its application became popular following the publication of Ptak and Schaeffer (1993), who advocated the use of a repeatability animal model. In the two-step approach, breeding values are estimated from lactation data using an animal model after correcting for environmental effects on the TD (Swalve 1998). The two step approach has been used in Australia (Jones 1985, Jones and Goddard 1990), New Zealand (Johnson 1996) and parts of United States (Everett *et al.* 1994, Stanton *et al.* 1992). In the study by Johnson (1996) estimates for the correction of HTD effects are calculated applying an extended version of Wood's IG model (Wood 1967).

Many studies showed that the linear-based routine method is satisfactory as long as its assumptions are fulfilled (Vargas *et al.* 2000, Ptak and Frącz 2002). However, methods based on lactation curve models (LCM) have some advantages over those used traditionally, as they deliver statistics useful in management, such as persistency of lactation, day of peak milk yield, as well as peak milk yield, and average curves for herd production (Schaeffer and Jamrozik 1996, Ptak *et al.* 2004).

The parameter estimates of lactation models contain genetic attributes which suggest that the shape of the lactation curve can be manipulated by selection (Ali and Schaeffer 1987).

Scheeberger (1981) and Ferris (1981) reported heritabilities of 0.07-0.14 for the parameters of the IG function. Ali and Schaeffer (1987) used three models and obtained h^2 estimates of initial milk yield ranging from 0.01 to 0.52 in first parity cows for the polynomial, inverse quadratic (Yadav *et al.* (1977) and IG models. The heritability of initial milk yield for the three models in second parity cows were 0.16, 0.00 and 0.12 respectively. Incline to peak yield h^2 estimates ranged from 0.15 to 0.61, 0.01 to 0.04 and 0.17-0.30, while that of the post-peak decline ranged from 0.07-0.35, 0.00-0.45 and 0.23-0.23 for the same models respectively.

Using the Bayesian approach, Rekaya *et al.* (2000) reported heritabilities of 0.23, 0.36 and 0.17 for parameters a , b and c of the IG model with genetic correlations -0.74, -0.49, and 0.69 between parameters a vs. b , a vs. c and b vs. c respectively. The corresponding phenotypic correlations were -0.6, 0.14 and 0.46 respectively. The parameters associated with peak milk yield i.e. $\log_e a$ (IG), Wood (1967), and β_1 (inverse quadratic polynomial (Yadav *et al.* (1977) had high positive correlations with 305-d milk yield while slope parameters had near zero or negative correlation (Ali and Schaeffer 1987). Large values of $\log_e a$ and b are necessary to improve response to selection on 305d milk yield. They also reported that genetic correlations between the same parameters at different lactations were low, for instance the correlation between milk yield in first and second lactations ranged between 0.17 and 0.37 contrary to values ≥ 0.97 earlier reported by (Tong *et al.* 1979). They explained that this result may be due to the smaller proportion of cows with first and second lactations in their data, 37.5% compared with 75% in typical herd composition. Furthermore they suggested that the PR model could be used to change the shape of the lactation curve without adversely changing 305d milk yield because there is good correlation among its parameters.

2.14.2 Covariance Functions

Covariance functions (CF) are the equivalent of covariance matrices for traits with multiple records in which the covariances are defined as a function of age or time. When using a multiple-trait approach, a covariance function offers the opportunity to reduce the rank of the covariance matrix among (highly) correlated traits from n (number of traits) to k (number of functions) (Swalve 2000). This is a two step approach in which a suitable smoothing function, e.g. a Legendre polynomial, is used to model the lactation curve and

the variances and covariances are estimated by the method of Kirkpatrick *et al.* (1990).. Ali and Schaeffer (1987) used the RRM approach to evaluate different covariances of daily milk yields and found out that accounting for covariances among daily yields did not improve the ability of the models to predict daily yields.

Meyer and Hill (1997) and van der Werf *et al.* (1998) demonstrated that CF can be equivalent to RRM if the same functions are used, i.e. when n traits are reduced to k functions, CF and RRM are equivalent to a multiple-trait model. A unique feature of the CF approach in genetic analysis is that the eigenvalues and eigenvectors have unique interpretations; for instance, the leading engenvalue corresponds to the constant coefficient of the polynomial (Meyer and Hill 1997).

2.14.3 Random regression test-day models

Random regression models (RRM) were introduced by Henderson (1982) and Laird and Ware (1982). Schaeffer and Dekkers (1994) suggested their use in dairy cattle breeding for the analysis of test-day production records. Random regression models have been used for genetic evaluation of dairy cattle for test-date milk production (Swalve 2000, Schaeffer *et al.* 2000, Jensen 2001), conformation traits, body condition scores (Berry *et al.* 2002), feed intake (Roche *et al.* 2006, Buckley *et al.* 2003), and heart girth measures in dairy cattle; weights and back fat thickness in swine and beef cattle; fork length and weights in rainbow trout; and litter size in swine. Other potential applications include: wool yield in sheep; sperm production and quality in male reproduction of any species; lifetime milk production in dairy cattle; genotype by environment interactions; survival analyses; and female reproduction (Schaeffer 2004). The general form of the RRM is discussed in Chapter 3.

There is on-going research to determine the order of fit for the random regressions for additive genetic and permanent environmental effects that account for high variation in TD observations. The use of functional models for the covariables of time has largely been abandoned in favour of orthogonal polynomials because the estimated covariance matrices, G and P , usually have very high correlations among the coefficients. In contrast, orthogonal polynomials of time have much lower correlations among the coefficients and provide estimates of the covariance matrices that tend to be more robust over different data sets. (Schaeffer 2004)

2.14.4 Character process models (CPM).

Another method of genetic evaluation, not pursued further in this thesis but described in the review by Jensen (2001), is the character process models (CPM) presented by Jaffrézic and Pletcher (2000) and Pletcher and Geyer (1999). In addition to modelling the random part of the trajectory of the lactation, the CPM is used to directly estimate the parameters in a model for the covariance structure. Based on the assumptions of correlation stationarity, where correlation is only dependent on the distance in age between two measures, the CPM generally leads to fewer parameters to estimate. According to the authors, the assumption of correlation stationarity can be relaxed by applying an appropriate transformation of the time scale (DIM).

2.15 Heritability estimates, genetic and phenotypic correlations of production traits

Production traits in dairy animals are controlled by multi-loci genes, some of which have dominant, epistatic or antagonistic relationships. Whereas milk yield is generally positively correlated with fat and protein yield, it is negatively correlated with livability and reproductive traits (Castillo-Juarez *et al.* 2000, Haile-Mariam *et al.* 2003). Until 2001, the Australian Selection Index (ASI), based on production traits, was used as the EBV of choice for ranking breeding bulls. The Australian Profit Ranking (APR), whose aim was to maximise profit from genetic gain by predicting the profitability of a bull's progeny according to the breeding objective, was introduced in 2001 (ADHIS 2001). Animal breeders are constantly exploring methods of predicting the genetic relationship between traits as a basis for genetic improvement and increasing profitability of the dairy industry.

Silvestre *et al.* (2005) fitted a spline animal model to 152,103 test-day milk, fat and protein yields of 14,423 first parity cows and reported milk yield heritability h^2 at 18 DIM to be 0.19, which increased to a maximum of 0.23 at mid lactation (138-198 DIM), then decreased to 0.21 until the end of lactation. Reported heritabilities of milk yield for test days 1 to 10 were 0.23, 0.25, 0.27, 0.28, 0.31, 0.30, 0.31, 0.31, 0.31 and 0.27, respectively. On the other hand, White *et al.* (1999) obtained h^2 estimates for protein starting at 0.17 at the on-set of lactation, increasing to 0.22 during mid lactation and then declined to 0.21 at the end of lactation, The h^2 of fat generally increased throughout lactation and ranged from 0.12 at 18 DIM to 0.19 at 348 DIM. Higher (Pander *et al.* 1992, 1993, Swalve 1995,

Jamrozik and Schaeffer 1997) and lower (Meyer *et al.* 1989, Veerkamp and Goddard 1998, Gengler *et al.* 1999; Tijani *et al.* 1999, Gengler *et al.* 2001) heritabilities of milk yield traits have also been reported. However, these researchers agreed that heritabilities of fat were, in almost all cases, lower than that of protein and that milk production has the highest h^2 .

White *et al.* (1999) fitted splines with 10 knot points corresponding to data from test-day milk yield records of 2885 progenies of 30 Holstein-Friesian sires in 503 herds and reported genetic and phenotypic variances (kg^2) which ranged from 2.93(DIM 109) to 3.45(DIM 290) and 9.59 (DIM 139) to 15.11 (DIM 18) respectively. The corresponding environmental and residual variances at DIM 139 and 18 were 6.00-9.10 and 2.25-5.17, respectively. Genetic and phenotypic correlations were strongest for adjacent test-day milk yield in early lactation which declined to the end of lactation and weakest for DIM far between. For instance, genetic correlation between TD1 and TD2 was 0.98 while that between TD1 and TD10 was 0.77. The corresponding phenotypic correlations for the same days were 0.64 and 0.40.

Phenotypic variance for milk yield was highest immediately post-partum at 30.09 declined to nadir at 18.69 (138d) before increasing to 29.95 at lactation end (Silvestre *et al.* 2005). Phenotypic fat yield followed a similar trend and ranged from 33.18 (138d) to 52.06 (18d) while phenotypic variance for protein was highest at the end of lactation (31.45) and lowest (18.30) at 138d. Genetic variances were 4.08 to 6.33, 4.19 to 8.59 and 3.34 to 6.68 for milk, fat and protein yields respectively. Brotherstone *et al.* (2000) and Kettunen *et al.* (2000) reported similar values of genetic and phenotypic correlations. Brotherstone *et al.* (2000) also reported negative genetic correlations for milk yield when two parametric functions (Wilmink 1987 and Ptak and Schaeffer 1993) were used

Tijani *et al.* (1999) estimated covariance functions for all days of lactation and concluded that genetic variance for milk yield increased with DIM, although Strabel and Misztal (1999) have reported a declining trend for the milk, fat, and protein. According to Olori *et al.* (1999), this variation may be because the estimates of the additive and permanent environmental components of variance for TD yields in a random regression model depend on the sub-model fitted.

2.16 Summary of Literature review

In conclusion therefore, great variation exists in reported goodness of fit of lactation models especially to individual cows and the reasons for these have been diverse. There is general consensus on the factors affecting curve shapes but some of these factors may be unique to production systems or environment. In addition there is general paucity of information not only on pasture-based systems but also on the usefulness of curve parameters for management decisions. Most of the studies that have evaluated the genetic parameters of production traits, with the exception of studies conducted in New Zealand, Australia and Ireland, have utilized data emanating from more intensive feeding systems. These constitute gaps which this thesis intends to fill the gap by evaluating the goodness of fit of different lactation functions using data from dairy herds in Tasmania. Factors affecting curves shapes will be evaluated with the best performing models and the potential of the model parameters for genetic improvement will be examined. Finally, this thesis intends to provide additional information that may be useful for management decisions under pasture-based systems.

Chapter 3 General Materials and Methods

3.1 Development of lactation models:

Lactation models are essential research tools for explaining the main features of the milk production pattern in terms of the known biology of the mammary gland during pregnancy and lactation (Macciotta *et al.* 2005; Neal and Thornley, 1983). Daily milk yield over the course of the lactation in dairy cows follows a curvilinear pattern (Silvestre *et al.* 2006), hence the need for a suitable function to model this curve. Consistent efforts have been made over the years to find appropriate and robust mathematical models which represent the lactation curve (Wood 1967, Ali and Schaeffer 1987, Wilmink 1987, Grossman and Koops 1988, Sherchand *et al.* 1995, Guo and Swalve 1995). The study of the mathematical properties of the lactation curve provides summarized information about dairy cattle production, which is useful in making management decisions (Bohmanova *et al.* 2008; Silvestre *et al.* 2006).

The thesis evaluated the fitness of pasture-based lactation data to empirical, mechanistic and non-parametric functions. Empirical models relate input to output without considering the intervening metabolism. In mechanistic models the response of the whole animal is simulated by the representation of individual tissue (Beever *et al.* 1991, Tozer and Huffaker, 1999). A brief overview of model development is here described as background to the choice of models that were used in the thesis.

3.2 Empirical models

The first attempt to model entire lactation was the incomplete *gamma* (IG) function (Wood 1967) which has the form

$$y_t = at^b \exp(-ct) \quad 3.1.1$$

Where average daily milk production (y_t) at time t is a function of “a”, a scaling factor representing yield at the beginning of lactation; b and c are factors associated with the inclining leading to peak yield and declining slopes post peak yield of the lactation curve.

The incomplete gamma function Wood (1967) is still one of the most commonly used models to fit milk test-day (TD) data, mainly because its three parameters can be related

to technical components of the curve. (Wood 1970, Wood 1972). *Typical* lactation curves have positive b and c . Curves with negative b or c are considered be *atypical* (Shimizu and Umrod 1976, Olori *et al.* 1999, Rekik and Ben Gara 2004, Macciotta *et al.* 2005). In chapter 5 the IG model was logarithmic transformed and solved by ordinary least squares analysis for multiple regressions as follows.

$$\ln(y_t) = \ln(a) + b \ln(t) - ct \quad 3.1.2$$

Other parameters of the IG model explored in chapters modelling lactation curve;

$$\text{Lactation persistency } p \text{ as } p = -(b+1) \log(c) \quad 3.1.3$$

$$\text{Time to peak yield } t_m \text{ as } t_m = b/c \quad 3.1.4$$

$$\text{Peak yield } y_m \text{ as } y_m = a(b/c)^b e^{-b} \quad 3.1.5$$

$$\text{Yield to time } n \quad y_n = a \int_0^n n^b \exp(-cd) dn \quad 3.1.6$$

$$\text{Total Yield } y = \frac{a}{c^{b+1}} \sqrt{(b+1)} \quad 3.1.7$$

The function $c^{-(b+1)}$, corresponds to the measure of “persistency” or the extent to which peak yield is maintained. If $S = c^{-(b+1)}$, the relationship between persistency and total yield and level of production is given by

$$\ln(y) = \ln(a) + \ln(S) + \ln(\Gamma(b+1)) \quad 3.1.8$$

For a given a or S therefore variations in y depend almost entirely on variations in S or a respectively.

Criticism of the IG model saw the emergence of other empirical models which were also tested in the thesis. These included the modified gamma (MG), Jenkins and Ferrel (1984), polynomial regression (PR), Ali and Schaeffer (1987) and the exponential (EXP) Wilmlink (1987) models. A brief background into the developments of these models is here given (see details in Beever *et al.* 1991).

Dhanao (1981), introduced a new parameter m equal to time to peak. This model achieved a lower correlation between parameters m and c compared to b and c in the original IG model.

$$y_t = at^{mc} \exp(-ct) \quad 3.1.9$$

ii) In order to account for seasonal effect on lactation in the northern hemisphere, Goodall (1983), suggested a categorical measure D equated to 0 and 1 for winter and summer production respectively.

$$y_t = at^b \exp(-ct + dD) \quad 3.1.10$$

where d estimates the seasonality factor. Lennox *et al.* 1992 suggested that this model is also suitable for modeling the effect of turning cows to pasture in spring.

iii) Jenkins and Ferrell (1984), proposed a two parameter model by setting the exponent of t , the value of b in the IG model equal to 1, resulting in a model which forced the rise to peak to begin at approximately zero irrespective of initial milk yields.

$$y_t = at \exp(-ct) \quad 3.1.11$$

In 1987 the polynomial PR and EXP models were proposed. The PR has the form

$$y_t = a + bt_1 + ct_2^2 + d \ln t_1 + e(\ln t_2)^2 \quad 3.1.12$$

where $t_1 = t/305$, $t_2 = \ln(305/t)$, a is a parameter associated with the peak yield, d and e are parameters associated with increasing slope, and b and c are associated with decreasing slope.

The EXP model, Wilmink (1987), has the form

$$y_t = a + bt + c \exp(-kt) \quad 3.1.13$$

where a represents the level at which production commences, b and c are the decline and incline phases respectively while k , a constant term estimated to be 0.05, is related to the time of peak milk yield which occurred around 50 days post partum in Dutch Friesian cows. Parameter k has been variously fixed at 0.61, (Olori *et al.* 1999), 0.1 (Macciotta *et al.* 2005), 0.19 (Macciotta *et al.* 2006), and 0.065 (Silvestre *et al.* 2006).

Although not used in the thesis, another significant model was the multiphasic logistical function (Grossman and Koops 1988). The model represented lactation as a multiphasic biological process and total milk yield as the sum of the yield resulting from each of the lactation phases. The model is of the form:

$$y_i = \sum_i^n \{a_i b_i [1 - \tanh^{-2}(b_i(t - c_i))]\} \quad 3.1.14$$

where n is the number of lactation phases considered and \tanh is the hyperbolic tangent. For each phase i , peak yield equals $a_i b_i$ and occurs at time c_i . The duration of each phase is related to $2b_i - 1$ which represents the time required to attain 75% of asymptotic total yield during that phase (Grossman and Koops 1988). Two forms of the model were presented: a diphasic and a triphasic form.

Other empirical models with varying degrees of complexity and number of parameters (Cobby and Le Du 1978, Batra *et al.* 1987, Papajcsik and Boderó 1988, Grossman *et al.* 1986, Morant and Gnanasakthy 1989, Guo and Swalve 1995, Weigel *et al.* 1992, Rook *et al.* 1993, Gengler 1996,) have been proposed. Eiston *et al.* (1989) proposed that the use of *non-parametric* lactation curves are statistically less biased than conventional *parametric* curves. The application of some lactation models to livestock data and parameter estimates are shown in appendix 1.

3.3 Mechanistic models of lactation

Limitations in the goodness of fit of empirical models (discussed in chapter 2) and the need to relate lactation to physiological process led to the development of mechanistic models. The basis of the mechanistic model was proposed by Neal and Thornley (1983).

In it the mammary gland was represented by undifferentiated cells which undergo division and differentiation leading to milk synthesis at or just before parturition. Milk synthesis is triggered by a single pulse of hormone at time zero and declines in response to death of cells and exponential decay of hormone. Figure 3.1 shows the schematic representation of the mechanistic model of lactation in mammals according to Neal and Thornley (1983).

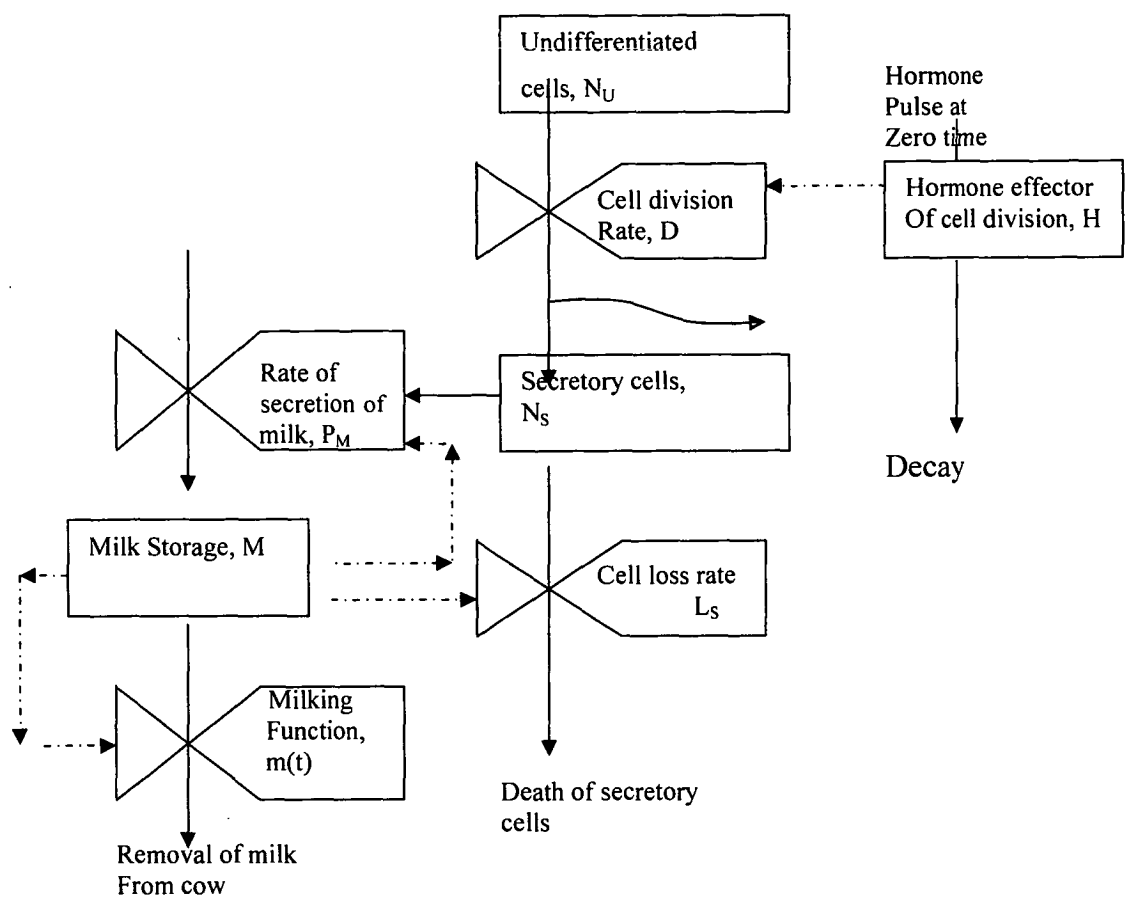


Figure 3.1. Mechanistic model of milk synthesis and secretion.
Boxes represent state variables; values denote processes of transformation, and broken lines indicate where variables are assumed to affect the rate of processes (Source: Neal and Thornley, 1983).

Ferguson and Boston (1993) presented two forms of a bi-compartmental (BC) model of lactation in dairy cows, one each for *typical* and *atypical* lactations respectively.

$$y(t) = ae^{-bt} + de^{-ct} \quad 3.1.15$$

$$y(t) = ae^{-ct} \quad 3.1.16$$

where a is related to the number of cells that undergo activation at time t , d is related to the variation of the number of activated cells at the same time, b and c are positive parameters that measure cell activation rate and secretory cell inactivation rate respectively. Equation 3.1.15 was fitted to pasture-based data in chapter 5.

Also utilized in chapter 6 was the Dijkstra (DJ) model which described the pattern of mammary growth of mammals throughout pregnancy and lactation (Dijkstra *et al.* 1997) and Pollott (PT) model (Pollott 2000). The DJ model has the form

$$Y_t = a \exp[b(1 - e^{-ct})/c^{-dt}] \quad 3.1.17$$

where a = theoretical initial milk yield, b = specific rate of secretory cell proliferation, c = decay parameter, d = specific rate of cell death. In addition to cell differentiation and death, the Pollott (2000) model included an additional process, milk secretion rate per cell, and has an additive and a multiplicative form viz.

$$y_i = a(1/(1 + \frac{1-b}{b}e^{-ct}) - k/(1 + \frac{1-d}{d}e^{-gt}))(1 - e^{-ht}) \quad 3.1.18$$

$$y_i = a(1/(1 + \frac{1-b}{b}e^{-ct}) - 1/(1 + \frac{1-d}{d}e^{-gt}))(1 - e^{-ht}) \quad 3.1.19$$

where y_i = daily milk yield, a = maximum or total milk secretion potential which is a function of total number of secretory cells produced and differentiated during the course of lactation excluding any secondary proliferation due to external stimuli and the maximum

secretion rate (kg/cell/day), b = the maximum number of secretory cells present at the start of lactation i.e. a measure of udder capacity which can be influenced by age, c = relative rate of increase in cell differentiation which describes the speed of increase in active cell numbers during pregnancy and lactation, k = maximum secretion loss (this component is reduced to 1 in the additive model because $a = k$, d = proportion of differentiated cells that have died by the start of lactation, g = the relative rate of decline in cell numbers, which is a measure of persistency of lactation and h = secretion rate. Other mechanistic models not used in the thesis are those of Emmans and Fisher (1986), Grossman and Koops (2003) and Pollott (2004).

Apart from empirical and mechanistic models scientists have begun in recent years to apply general mathematical tools, including Legendre polynomials (Kirkpatrick *et al.* 1994, Ptak *et al.* 2004) and splines (White *et al.* 1999, Macciotta *et al.* 2005, Silvestre *et al.* 2006) to model lactation in dairy cows. Although legendary polynomials (LPs) are orthogonal, easy to fit, and linear as functions of parameters (Pool *et al.* 2000), their parameters have no biological meaning (Ptak *et al.* 2004).

3.4 Test-day models

Test-day models are defined as statistical procedures in which both genetic and environmental effects are considered to affect each test-day. Test day milk yields recorded at different ages represent a case of repeated measures in time which can be analyzed as repeated measures, multiple traits or random regression models, (see justifications and background for random regression models in chapter 2). The method was initially suggested by Henderson (1982), but popularized by Schaeffer and Dekkers (1994) who suggested its use in analyzing TD records where each test-date is treated as a repeated measure of the same trait or as a separate trait. Two estimable forms; a repeatability model (Meyer *et al.* 1987, Ptak and Schaeffer 1993), and bi-variate animal model (Swalve 1998) were utilized in the chapter on factors affecting the shape of lactation curves and estimation of genetic parameters of the IG function.

In general scalar notation the repeatability model is given as

$$Y_i = Xb + Za + Wp + e \quad 3.1.20$$

where Y_i is the vector of observations, b is the vector of fixed effects including; herd-test-date (HTD), calving year and season, parity and age class, a is the vector of random additive genetic effect of the animal, p is the vector of permanent environment effects associated with each lactation, e is the vector of random residual effects, and X , Z , and W are the incidence and covariable matrices. The permanent environmental effect and residual are assumed not correlated with means=0 and variance σ_p^2 and σ_e^2 respectively. The variance covariance matrix of the random effects are

$$\text{Var}(p) = I\sigma_p^2; \text{Var}(e) = I\sigma_e^2; \text{Var}(a) = A\sigma_a^2; \text{Var}(y) = ZAZ'\sigma_a^2 + WI\sigma_p^2W' + R$$

The variance of the observations comprises the variance due to genetic, permanent environment and random temporary effects. The correlation between records of an animal also known as the repeatability is $r = (\sigma_a^2 + \sigma_p^2) / \sigma_y^2$

Similar equation and model terms as 3.1.20 apply for the bivariate animal model except that the G-structure is a product matrix as presented below.

Assume that

$$y|b, a, p, \sigma_e^2 \sim N(Xb + Za + Wp, R), \text{ and}$$

$$\begin{pmatrix} a \\ p \\ e \end{pmatrix} \sim N(0, V)$$

with G structure

$$\begin{pmatrix} G \otimes A & 0 & 0 \\ 0 & I\sigma_p^2 & 0 \\ 0 & 0 & U \end{pmatrix}$$

where G is covariance matrix of the random regression coefficients, assumed to be the same for all cows; A is additive genetic relationship matrix among the animals; \otimes is

Kronecker product function (Searle 1982); I is identity matrix; and U is unstructured matrix with elements that define the two traits.

The mixed model equation for this model would be

$$\begin{pmatrix} X'R^{-1}X & X'R^{-1}Z & X'R^{-1}W \\ Z'R^{-1}X & Z'R^{-1}Z + G^{-1} \otimes A^{-1} & Z'R^{-1}W \\ W'R^{-1}X & W'R^{-1}Z & W'R^{-1}W + Ik \end{pmatrix} \begin{pmatrix} \hat{b} \\ \hat{a} \\ \hat{p} \end{pmatrix} = \begin{pmatrix} X'R^{-1}y \\ Z'R^{-1}y \\ W'R^{-1}y \end{pmatrix}$$

where $k = I / \sigma_p^2$ which was assumed constant across traits. The R-structure which was

assumed correlated is described in matrix notation as $R = I \otimes \begin{bmatrix} \sigma_1^2 & \sigma_{12} \\ \sigma_{12} & \sigma_2^2 \end{bmatrix}$

The curve of the lactation was accounted for with either legendre polynomial (Chapter 6) or cubic splines (Chapter 7). The regressions were nested within classes of fixed effects and a separate covariance structure accounted for the heterogeneity of residual variance. Test day models have also been treated as multiple-trait models under which individual TD records are considered as separate traits. (Reents *et al.* 1995a, Reents *et al.* 1995b).

3.5 Semi parametric models

The use of functional trait models with fixed or random coefficients represents a form of parametric model. Non-parametric or semi-parametric curves including Legendre polynomials (Kirkpatrick *et al.* 1990) and cubic splines White *et al.* 1999) have been suggested for genetic evaluations in lactation modeling. These functions, analogous to quadratic and higher order terms in a polynomial, were incorporated into random regression models to compare their goodness of fit to milk constituent yields from two pasture-based production systems in chapter 5.

3.5.1 Legendre polynomials

Legendre polynomials (LEG) are polynomial functions of n degree and domain $n + 1$ and the equation describing a single observation can be written as:

$$Y_i = \sum_{i=0}^n \alpha_i \phi_i(w) \quad 3.1.21$$

where w standardized unit of time ranging from -1 to +1. For a given set of test day milk yields y recorded on test-dates x , where minimum and maximum DIM are respectively 5 and 305 (Schaeffer 2004), w is represented as

$$w = 2 \left(\frac{t - t_{\min}}{t_{\max} - t_{\min}} \right) - 1 \quad 3.1.22$$

and

$$\phi_n(w) = \sqrt{\frac{2n+1}{2}} P_n(w) \quad 3.1.23$$

where $P_n(w)$ is a polynomial of degree n and $\phi_n(w)$ is the normalized polynomial. LEG are orthogonal, easy to fit and linear as functions of parameters (Pool *et al.* 2000).

3.5.2 Cubic splines

A cubic spline is a smooth curve over an interval formed by linked segments of cubic polynomials at certain knot-points, so that the whole curve and its first and second differentials are continuous over the interval (Green and Silverman, 1994). Verbyla *et al.* (1999) demonstrated that cubic splines are particularly convenient because they can be incorporated into a suitably constructed mixed model framework (White *et al.* 1999, Silvestre *et al.* 2005), while Swalve (2000) and Guo and Schaeffer (2002) classified the spline model as a random regression test-day model with the spline function being a sub model of the lactation curve. The ASReml software (Gilmour *et al.* 2002) has made the computations practical thus enabling White *et al.* (1999) and Silvestre *et al.* (2005) to apply this methodology to estimate genetic parameters for dairy cow lactation curves. According to Jensen (2001), spline models applied to test-day data are a class of TD models.

In suffix notation the mixed model for a single spline equation can be represented as

$$y_j = b_0 + b_1 t_j + \sum_{k=2}^{q-1} v_k z_k(t_j) + e_j \quad 3.1.24$$

$j=1 \dots n$

where y_j =observation on milk yield, and t_j =lactation stage (DIM) for a particular animal at test j . The term v_k represents the estimate for a mean spline-coefficient at the knotpoint k , q is the number of knots and z_k is the random spline-coefficient for test day t_j . Suppose there are m animals and that animal i enters test j at t_{ij} DIM. Test j measurement for animal i ($j = 1, \dots, n_i$) will be y_{ij} . Then, a natural extension of the spline model becomes

$$y_{ij} = b_0 + b_1 t_{ij} + b_{i0} + b_{i1} t_{ij} + \sum_{k=2}^{q-1} v_k z_k(t_{ij}) + \sum_{k=2}^{q-1} v_{ik} z_k(t_{ij}) + e_{ij} \quad 3.1.25$$

where the first two terms represent an overall linear regression, the third and fourth terms (animal and animal x linear) describe the deviation from the overall regression for animal i , and the fifth and sixth terms (spline and animal x spline) represent, respectively, a mean spline deviation and the deviation from the mean spline for animal i . The final term e_{ij} is the residual error with variance σ_e^2 . The parentheses are ANOVA expressions for the individual terms in which spline is shorthand for the joint effect of the covariates $z_2(t), \dots, z_{q-1}(t)$ (White *et al.* 1999). The equation is identical to random regression models with covariates t and $z_j(t)$, $j=2 \dots q-1$ where polynomials of increasing degree or a set of unrelated functions of DIM, i.e., t^2 , $\log(t)$, are replaced by $z_2(t)$ which represent a sequence of shifted curves.

3.6 Model evaluation:

Models are predictive and the usefulness of a model depends on how well it represents the physiological basis of lactation and adjusts for environmental factors affecting it. Various

methods have been used to evaluate the goodness of fit of lactation models. Some of those used in this thesis include adjusted R^2 , calculated as $R^2=100*[1-(\text{residual mean square}/\text{Total mean Square})]$ (Olori *et al.* 1999), the plot of residuals against lactation stage, correlation of residuals with observed yields and correlation of predicted with observed yields. The latter can be further assessed with the mean square prediction error calculated as:

$$MSPE = \sum_{i=1}^n (O_i - P_i)^2 / n \quad 3.1.26$$

where $i = 1, 2, \dots, n$, n is the number of experimental observations, and O_i and P_i are the observed and predicted values, respectively. The Marquardt (Marquardt 1963) method algorithm in SAS is often used for non-linear models especially where the parameters to be estimated are highly correlated (SAS 2002). The F-test is used to test the significance of analysis of variance of the parameter estimates with the effects of known factors that affect milk yield. The Durbin-Watson test (Durbin 1970) is also a useful measure of model fitness however, the usefulness of this statistic is severely limited by its lack of sensitivity when testing for autocorrelation for models based on <15 observations (Durbin 1970)

Other tests of model fitness are the significance level of the parameters estimated, variance of error estimate, and its standard error. Comparison between models is also made using Bayesian information criteria (**BIC**) (Leonard and Hsu, 2001). Given a model with a number of explanatory variables, the fitness of the model depends on the number of parameters fitted. Bayesian information criteria are model-order selection criteria based on parsimony and impose a penalty on more complicated models for inclusion of additional parameters. The model with the smaller BIC value is to be preferred. Let:

- n = the number of observations, or equivalently, the sample size;
- k = the number of free parameters to be estimated. If the estimated model is a linear regression, k is the number of regressors, including the constant;
- L = the maximized value of the likelihood function for the estimated model.

BIC is given as

$$BIC = -2 \ln L + K \ln(n) \quad 3.1.27$$

Under the assumption that the model errors or disturbances are normally distributed, the equation can be described as a function dependent on n and not on the model as follows.

$$BIC = n \ln\left(\frac{RSS}{n}\right) + K \ln(n) \quad 3.1.28$$

where RSS is the residual sum of squares from the estimated model.

3.7 Genetic evaluation

In the traditional sire evaluation technique the 305-d or adjusted 305-d milk yield is used in the estimation of an index, based on production of contemporary groups, which is then used to derive the breeding values. On the other hand the lactation curve method is a two-step approach in which the lactation curve parameters for an individual cow are first estimated using the standard lactation curve. Breeding values are then subsequently estimated by accounting for covariances among test-day yields (Van Raden 1997).

Other approaches, such as random regression models or, equivalently, covariance function models can estimate genetic merit as a function of time, thereby allowing genetic selection for the shape of the lactation curve (Meyer and Hill 1997). However, these models do not allow direct inferences about genetic parameters of lactation curve functions, such as persistency, peak yield, and DIM at peak day (Rekaya *et al.* 2000).

3.8 Data sets and Editing

Three main data sources were utilised in testing the hypothesis examined in this thesis. These were the Tasmanian dairy herd data provided by Tasher Company which comprised of data from about 230 herds. Additional data were from experiential stations; Elliott Research and Demonstration Station (ERDS), Tasmania and Ellinbank dairy herd Victoria. All data sets were edited to exclude cows with unknown birth and or calving dates or with lactation length less than 100 days or days in milk < 4 . Records of DIM ≥ 306 but not the

cows were also excluded from the ananalysis. Additional details of data editing are given in the respective chapters.

3.9 Statistical analysis

In chapters 4 and 5, the least square means of week in milk for herd data were obtained before fitting the test-day data to the corresponding lactation function using the Marquardt's iterative method of the non-linear (NLIN) procedures of SAS (SAS 2002). Individual cow's test-day data were fitted to the lactation function using the actual week in milk. Parameter estimates were compared only within models and across data sets (where more than one data set was used). Evaluation of the models' accuracy was based on its ability to converge, on RMSE, the magnitude and distribution of residuals and the correlation between observed and predicted milk yield. Parameter k in the exponential model (Wilmink 1987) was fixed at 0.46, this being the best fitting value for herd mean yield of the data sets. Initial values for the procedures were obtained from the log transformed linearised analysis.

In chapter 5 to evaluate the effect of choice of sire breeding values on the shape of the lactation curve, the IG model was logarithmically transformed (Eqn 3.1.2); and solved by ordinary least squares analysis for multiple regressions using the regression procedures (PROC REG) of SAS (SAS 2002). Least square mean estimates for week in milk (WIM) were computed using PROC GLM (SAS 2002) to fit herd data while WIM from test-dates were used for individual curve fits.

Chapter 4. Genetic, physiological and herd management factors influencing milk, protein and fat yields of Pasture-based dairy cows in Tasmania, Australia

4.1 Summary

This chapter is an overview of the dairy production system in Tasmania. The objective was to determine the influence of genetic and non-genetic factors on milk, protein and fat yields of pasture-based dairy cows as a basis for lactation modelling. We conclude that herd size, location, breed, parity, season and year of calving were among the main factors driving production of dairy cows in Tasmania and adjustments for these factors would be mandatory for any unbiased comparison of lactation performance within and between pasture-based dairy production systems. Incomplete pedigree records affected the genetic estimates because nearly one third of the data were discarded because of missing sire identification.

4.2 Introduction

The dairy industry in Australia is very important to the agricultural sector of the economy. With an ex-factory value of \$9.1 billion and farm gate value of \$3.2 billion, it is the third biggest rural industry behind beef and wheat (Dairy Outlook 2006). Milk production is concentrated in the south-east corner of Australia, with the states of Victoria, Tasmania and South Australia accounting for 78% of the national output. Like in most states of Australia, dairying in Tasmania is characterized by seasonal, low-input pasture-based milk production reliant on family labour. However deregulation of the production sector in 2000 as well as widespread drought in 2002-03 led to substantial restructuring such as reduction in farm numbers, high cost of grain supplements and increased herd sizes (ABARE 2003). Although the Holstein-Friesian (FF) constitutes about 70% of the dairy breeds, there are growing numbers of other breeds including the Jersey (JJ), crossbreds of Holstein-Friesian and Jerseys (FJ), Guernsey (GG), Ilawara (II) and Australian reds (RR). Climatic factors also differ between dairy locations. The economic advantage of Australia in the global milk trade stems from its predominant pasture-based production system with fodder from pasture accounting for almost 60% of dairy cow feed (Dairy Outlook 2006). However, ninety percent of dairy farms use supplementary feeds such as hay, silage and concentrate to augment seasonal shortages

in grass production. Although production from Tasmania constitutes a small proportion of national output, nearly 90% of the milk produced in Tasmania is processed for export (Dairy Outlook 2006), compared to 30-40% in New South Wales (NSW), Queensland and Western Australia. Industry growth also indicates that the Tasmanian dairy industry is growing at rates comparable to those of the major dairy producing states of Australia. Tasmania's climate offers an opportunity for year round-milk production, where precipitation is not limiting. Consequently, dairy production in Tasmania will continue to play a significant role in both local and overseas export of milk products.

Milk is synthesized by secretory cells in the mammary glands of lactating animals primarily as nutrition for the young. Factors affecting milk production in dairy animals include genetic (Tekerli *et al.* 2000), environmental and management factors (Payne and Wilson 1999; Msanga *et al.* 2000). Several studies (Madgwick and Goddard 1989; Doyle and Kelly; 1998, Dobos *et al.* 2001; Wales *et al.* 2006) have identified factors affecting milk production of dairy cows in Victoria and other parts of Australia. However, except for some performance indicators of the industry compiled by the Department of Primary Industry and Water (Dairy Outlook 2006, see appendix 4.1) and Dairy Australia (2005), there is paucity of recent information in the scientific literature about the dairy industry in Tasmania. Therefore, the objectives of this study were to characterize the milk production of pasture-based dairy cows in Tasmania as influenced by breed, parity, location, herd size, season, parity, year and their interactions and to identify the critical management factors underpinning milk and milk component yields.

4.3 Materials and methods

4.3.1 Site and climatic conditions

Tasmania is Australia's southern-most state with a land mass of 68,000 sq km, located at latitude 42° South, longitude 147° East and completely within the temperate zone. The seasons are different from those of the Northern Hemisphere in that summer is from December to February, autumn from March – May, winter from June – August and spring from September – November. Average maximum temperatures are 21⁰C (70⁰ F) and 12⁰C (54⁰ F) in summer and winter respectively. Summer is warm with sunny days and mild evenings, while autumn is cool with frosty nights and occasional storms. Winter is mild with occasional snows on the higher mountain peaks. The annual rainfall

varies from 626 millimeters (25 inches) in Hobart to 2,400 millimeters (94 inches) on the West Coast. The prevailing weather pattern creates a rain shadow in the west to east direction leaving the East Coast always warmer and drier than the rest of the state.

4.3.2 Data source and editing

The data used in this study were obtained from TasHerd, which is the contracted herd recording agency for the Australian Dairy Herd Improvement Scheme (ADHIS) in Tasmania. The data were from 428 dairy herds and consisted of 130,366 observations on 305 day milk, fat, protein and somatic cell count (SCC) yield records of purebred Holstein-Friesian (FF), Jersey (JJ), Guernsey, Illawarra, and Australian Reds, as well as crosses of Holstein-Friesian and Jersey (FJ) cows of different ages, season of calving, parity, and lactation length. The \log_e of the somatic cell count data was obtained to normalise the somatic cell count trait.

Two data sets were formed. DATA1, which explored the factors affecting production traits, used records from three breeds, namely FF, JJ and FJ, as these constitute the predominant breeds in Tasmania. Small data size and incomplete pedigree records for some cows and on the other breeds and regional data made heritability estimation difficult; hence, only records from the FF breed were utilized for genetic analysis in DATA2. For each cow, records of cow number, birth date, calving date, 305d milk and milk components yields, lactation length, and herd number were available. This information was used to determine cow age, calving season, parity, and herd sizes. Lactations with incomplete records, i.e. missing; birth date, calving date, milk or component yields were deleted. Records of cows with lactation length <100 days were also excluded from the analysis. The final data set DATA1 consisted of 106,990 records of observations from 428 herds over six production years. The data consisted of cows in first to 9th parity. Parities greater than four constitute about 22% of the entire data and were collectively referred to as parity >4. The classification did not affect the class of calving year, season and other fixed effects. To protect farm identities, dairy farm's coded herd numbers and postcodes were used. The final data set consisting of thirty postcodes was divided into 6 subsets, herein referred to as locations, based on existing local council areas which have been delineated by geographical contiguity. For instance, herds with postcodes 7260-7265 were grouped into the North East location (Table 4.1).

Herds were classified according to sizes such that there were approximately equal numbers of herds in each class. Four herd size classes were defined, viz. 1-210, 211-575, 576-1100 and >1100 cows per herd, designated as small, medium, large and very large herds, respectively. Additional data omitted from the analysis of DATA2 were all breeds except FF, cows with parity >5 and 305d milk yield <1,200L, leaving a total of 65,914 records. Parities >2 were pooled and labelled as Parity3. Dairy farm statistics of Tasmania are presented in appendix 4.1. Least squares means and summary statistics of the traits for DATA1 and DATA2 are presented in Tables 4.1 and 4.3 respectively.

4.3.3 Statistical analysis

The general linear models (GLM) procedure in SAS (SAS 2002) was utilised to compute least squares means, standard errors and coefficient of variation of the traits in DATA1. Location, herd size, breed, calving year, calving season and parity were used as fixed effects while age and lactation length were included as covariates. All possible interactions between the fixed effects were included in the original model but non significant interactions were dropped from the final model. The model used to describe each lactation record was:

$$Y_{ijklmnopq} = \mu + L_i + H_j + S_k + Y_l + B_m + P_n + (BS)_{km} + (BY)_{lm} + (SP)_{kn} + (BP)_{mn} + (PSY)_{nkl} + b_1(L_{ijklmno} - \bar{L})^2 + b_2(A_{ijklmnop} - \bar{A})^2 + e_{ijklmnopq} \quad 4.1$$

where $Y_{ijklmnopq}$ is the $ijklmnopq$ observation of the trait in question, with fixed effects; L_i of i^{th} location ($i=1,2...6$), H_j of j^{th} herd size ($j=1,2...4$), S_k of k^{th} season of calving ($k=1,2...4$), Y_l of l^{th} year of calving ($l=1,2...6$), B_m of m^{th} breed ($m=1,2...3$), and P_n of n^{th} parity ($n=1,2...5$), first order interaction effects; $(BS)_{km}$ of breed and season, $(BY)_{lm}$ of breed and year, $(SP)_{kn}$ of season and parity and $(BP)_{mn}$ of breed and parity, second order interaction effect $(PSY)_{nkl}$ of parity, season and year, with partial regression coefficients b_1 of lactation length and b_2 of cow age, $(L_{ijklmno} - \bar{L})^2$ is the lactation length fitted as a covariate, $(A_{ijklmnop} - \bar{A})^2$ is the age of cow fitted as a covariate, μ is the overall mean and $e_{ijklmnopq}$ is a random sampling effect of lactation p with mean zero and variance σ_e^2 . Means were compared using the least significant difference technique of the SAS GLM procedure

DATA2 was used for the genetic analysis of milk, fat, protein and somatic cell count with Y, P, S, Herd (H) and YS interaction as fixed effects while cow was used as a random effect. Age at calving (Age) and lactation length (LL) were included as covariates in all analyses. All traits were first analysed with a univariate animal model in ASReml (Gilmour *et al.* 2006) to obtain start-up values for the covariance structures in subsequent analyses. Convergence difficulties arising from incomplete data across fixed effect groups made a single multivariate analysis impossible. Consequently, a series of bivariate analyses were performed in ASReml to estimate heritabilities, as well as phenotypic (rp) and genetic (rG) correlations of the traits (Tables 4.4 and 4.5). The average of any paired estimates of the trait were then used i.e. the average of heritability of milk yield obtained from the bivariate analysis of milk vs. fat and milk vs. protein content was used as the h^2 of milk yield.

The full model was

$$y_{ij} = \mu_i + Y_{ik} + P_{il} + S_{im} + YS_{ikm} + H_{in} + \beta_1 LL_j + \beta_2 Age_j + a_{ij} + e_{ij} \quad 4.2$$

where i represents the traits total milk, fat, protein and log of SCC, μ_i is the population mean for trait i , y_{ij} is the observation of trait i for cow j , Y_{ik} , P_{il} , S_{im} , YS_{ikm} , and H_{in} are the fixed effects of the traits on k^{th} calving year ($k=1,2 \dots 6$), l^{th} parity ($l=1,2 \dots 3$), S^{th} calving season ($S=1,2 \dots 4$), YS^{th} first order interaction of calving year and season ($YS=1,2 \dots 46$), H^{th} herd ($H=1,2 \dots 216$), respectively, β_1 and β_2 are the regression coefficients of lactation length (LL) and age at calving (Age) respectively, on trait i , a_{ij} is the random additive genetic effect on trait i for animal j and e_{ij} is the random residual error of trait i for individual j . A pedigree file tracing ancestry to the last five generations was included in the analysis of DATA2. There were 30,325 animals in the pedigree file.

In matrix notation the model can be written as

$$y = Xb + Za + e, \quad 4.3$$

where \mathbf{b} includes the fixed effects Y_{ik} , P_{il} , S_{ik} , YS_{ikm} , H_{in} , $\beta_1 LL_j$ and $\beta_2 Age_j$, \mathbf{a} includes a_{ij} , \mathbf{p} is the vector of permanent environment effects for cows with 305 day records,

\mathbf{e} is the vector of residual effects, and \mathbf{X} and \mathbf{Z} are the incidence and covariable matrices. Assume that

$$\mathbf{y}|\mathbf{b},\mathbf{a},\sigma_e^2 \sim N(\mathbf{Xb} + \mathbf{Za}, \mathbf{R}),$$

and

$$\begin{pmatrix} \mathbf{a} \\ \mathbf{p} \end{pmatrix} \sim N(0, \mathbf{V})$$

with

$$\mathbf{G} = \mathbf{A} \otimes \begin{bmatrix} \sigma_1^2 & \sigma_{12} \\ \sigma_{12} & \sigma_2^2 \end{bmatrix}$$

where \mathbf{G} is the product of the additive genetic relationship \mathbf{A} assumed to be the same for all cows and the covariance matrix coefficients \otimes is the Kronecker product function (Searle 1982).

The mixed model equation for this model is as defined in Chapter 3

4.4 Results

4.4.1 DATA1: Factors affecting milk and milk component yields

Results of total milk, fat, protein, milksolids and somatic cell count yields and their interactions are presented in Tables 4.1 and 4.2. Production traits differ between breeds, parity and season of calving, although fat, protein and somatic cell count (SCC) did not significantly differ ($p>0.05$) between the winter and summer seasons. The model (Equation 4.1) tested explained 40-43% of the variations due to genetic, environmental and management factors. Lactation length accounted for about 19.3% of the total sum of squares. The other factors influencing productivity were herd size, breed, parity, location, calving season and age in order of decreasing magnitude except for fat and protein yields where parity had greater influence than genotype and location. Breed, breed x year and parity x season did not significantly ($P>0.05$) affect somatic cell count.

Table 4.1. Least squares means (\pm s.e) of total milk, fat, protein yields per lactation and somatic cell count of dairy cows by breed, parity, calving year, location, herd size, and calving season.

Category	Milk (L)	Fat(kg)	Protein(kg)	Milksolids (kg)	Log SCC $\times 10^3$	Milk (Litre/d)	Milksolids (kg/d)	N*
Breed								
Cross	4253 \pm 53.7 ^b	196 \pm 2.1 ^b	150 \pm 1.7 ^b	346 \pm 3.7 ^b	135 \pm 10.4 ⁰	14.9 \pm 0.18 ^b	1.21 \pm 0.012 ^b	10,001
Friesian	5212 \pm 34.2 ^a	210 \pm 1.3 ^a	171 \pm 1.1 ^a	380 \pm 2.4 ^a	133 \pm 6.4 ^a	18.2 \pm 0.11 ^a	1.33 \pm 0.008 ^a	82,920
Jersey	3713 \pm 60.0 ^c	197 \pm 2.4 ^b	143 \pm 1.9 ^c	340 \pm 4.2 ^b	127 \pm 11.3 ^b	13.1 \pm 0.20 ^c	1.19 \pm 0.014 ^b	14,059
Parity								
1	3482 \pm 53.8 ^e	158 \pm 2.1 ^e	119 \pm 1.8 ^e	277 \pm 3.7 ^e	157 \pm 10.4 ^a	12.3 \pm 0.18 ^c	0.98 \pm 0.129 ^c	26,893
2	4020 \pm 45.2 ^d	184 \pm 1.8 ^d	141 \pm 1.5 ^d	326 \pm 3.1 ^d	132 \pm 8.5 ^b	14.2 \pm 0.15 ^d	1.15 \pm 0.011 ^d	22,372
3	4615 \pm 48.6 ^c	212 \pm 1.9 ^c	164 \pm 1.6 ^c	376 \pm 3.4 ^c	129 \pm 9.1 ^{bcd}	16.2 \pm 0.17 ^c	1.31 \pm 0.012 ^c	18,154
4	4826 \pm 51.6 ^b	222 \pm 2.0 ^b	172 \pm 1.7 ^b	393 \pm 3.6 ^b	127 \pm 9.7 ^{bd}	16.9 \pm 0.18 ^b	1.37 \pm 0.012 ^b	15,081
>4	5019 \pm 51.9 ^a	228 \pm 2.0 ^a	179 \pm 1.7 ^a	407 \pm 3.6 ^a	112 \pm 9.8 ^{cd}	17.5 \pm 0.18 ^a	1.42 \pm 0.012 ^a	24,490
Calving Year								
2000	4058 \pm 71.9 ^e	184 \pm 2.8 ^e	140 \pm 2.4 ^e	325 \pm 5.0 ^e	121 \pm 13.5 ^{bc}	14.3 \pm 0.25 ^d	1.41 \pm 0.017 ^a	6,064
2001	4299 \pm 54.5 ^d	196 \pm 2.1 ^d	150 \pm 1.8 ^d	346 \pm 3.8 ^d	115 \pm 10.2 ^c	15.1 \pm 0.19 ^c	1.21 \pm 0.013 ^d	9,447
2002	4406 \pm 49.3 ^c	200 \pm 1.9 ^c	153 \pm 1.6 ^{cd}	353 \pm 3.4 ^c	125 \pm 9.2 ^{bc}	15.4 \pm 0.17 ^c	1.23 \pm 0.012 ^d	13,334
2003	4305 \pm 44.9 ^d	198 \pm 1.8 ^{cd}	153 \pm 1.5 ^c	352 \pm 3.1 ^c	137 \pm 8.4 ^b	15.1 \pm 0.15 ^c	1.23 \pm 0.011 ^d	18,332
2004	4577 \pm 43.4 ^b	209 \pm 1.7 ^b	164 \pm 1.4 ^b	373 \pm 3.0 ^b	135 \pm 8.1 ^b	16.0 \pm 0.15 ^b	1.31 \pm 0.010 ^c	25,250
2005	4710 \pm 41.2 ^a	216 \pm 1.6 ^a	169 \pm 1.4 ^a	385 \pm 2.9 ^a	156 \pm 7.7 ^a	16.5 \pm 0.14 ^a	1.34 \pm 0.009 ^b	34,563
Location								
FNWest	4879 \pm 25.8 ^a	220 \pm 1.0 ^b	172 \pm 0.8 ^a	391 \pm 1.8 ^a	119 \pm 4.8 ^b	16.9 \pm 0.09 ^a	1.36 \pm 0.006 ^a	52,771
NWest	4498 \pm 27.2 ^c	206 \pm 1.1 ^d	159 \pm 0.9 ^c	365 \pm 1.9 ^c	129 \pm 5.1 ^a	15.8 \pm 0.09 ^c	1.28 \pm 0.006 ^c	25,574
CntNorth	4814 \pm 31.8 ^b	220 \pm 1.3 ^a	170 \pm 1.0 ^b	392 \pm 2.2 ^a	124 \pm 6.0 ⁰	16.7 \pm 0.11 ^b	1.36 \pm 0.008 ^a	4,931
South	4047 \pm 60.5 ^d	183 \pm 2.4 ^e	143 \pm 2.0 ^d	326 \pm 4.2 ^d	119 \pm 11.4 ^a	14.3 \pm 0.21 ^d	1.15 \pm 0.014 ^d	659
NEast	4786 \pm 26.8 ^b	213 \pm 1.1 ^c	168 \pm 0.9 ^b	382 \pm 1.9 ^b	119 \pm 4.8 ^b	16.7 \pm 0.09 ^b	1.33 \pm 0.006 ^b	26,997
King Isl.	3331 \pm 178 ^e	160 \pm 7.0 ^f	118 \pm 5.9 ^d	277 \pm 12.4 ^e	178 \pm 33.4 ^a	11.9 \pm 0.61 ^e	0.99 \pm 0.042 ^e	1058
Herd Size								
Large	4271 \pm 39.3 ^c	200 \pm 1.5 ^b	151 \pm 1.3 ^c	350 \pm 2.7 ^b	122 \pm 7.4 ^b	15.0 \pm 0.13 ^c	1.23 \pm 0.009 ^b	28,228
V. large	4672 \pm 39.2 ^a	212 \pm 1.5 ^a	166 \pm 1.3 ^a	378 \pm 2.7 ^a	131 \pm 7.4 ^a	16.4 \pm 0.13 ^d	1.32 \pm 0.009 ^a	71,509
Medium	4141 \pm 41.6 ^d	195 \pm 1.6 ^c	148 \pm 1.4 ^d	343 \pm 2.9 ^c	130 \pm 7.8 ^a	14.5 \pm 0.14 ^d	1.20 \pm 0.010 ^c	5,766
Small	4485 \pm 52.4 ^b	196 \pm 2.0 ^c	155 \pm 1.7 ^b	350 \pm 3.6 ^b	142 \pm 9.8 ^a	15.9 \pm 0.18 ^b	1.23 \pm 0.013 ^b	1,487
Calving Season								
Autumn	4094 \pm 42.4 ^c	189 \pm 1.7 ^c	144 \pm 1.4 ^c	333 \pm 2.9 ^c	112 \pm 8.0 ^c	14.6 \pm 0.15 ^c	1.18 \pm 0.010 ^c	10,130
Spring	4770 \pm 34.5 ^a	215 \pm 1.4 ^a	168 \pm 1.1 ^a	383 \pm 2.4 ^a	139 \pm 6.5 ^a	16.6 \pm 0.12 ^a	1.34 \pm 0.004 ^c	40,185
Summer	4249 \pm 94.4 ^c	190 \pm 3.7 ^c	148 \pm 3.1 ^c	338 \pm 6.6 ^c	146 \pm 17.4 ^{abc7}	14.8 \pm 0.32 ^c	1.18 \pm 0.023 ^c	1,584
Winter	4457 \pm 33.7 ^b	208 \pm 1.3 ^b	160 \pm 1.1 ^b	368 \pm 2.3 ^b	129 \pm 6.3 ^b	15.6 \pm 0.12 ^b	1.29 \pm 0.008 ^b	55,091

All tested factors were significant $P < 0.0001$, *N=Number of observationsMeans bearing different superscripts within the same column are statistically different ($p < 0.001$)

Locations = Far North West, North West, Central North, South, North East and King Island respectively.

SCC= Somatic cell count

4.4.2 Genetic factors

Breed

Milk yield was significantly different ($p < 0.0001$) between the three breeds evaluated in this study (Table 4.1). Total milk, fat, protein and milksolids yields were highest in FF and lowest in JJ cows. The maximum differences between the three genotypes in milk, fat and protein yields were 1499 litres, 14 kg and 27.7 kg respectively. FF and FJ cows produced milk with significantly higher content of SCC than JJ cows. JJ and FJ cows produced 28.8% and 18.4% less milk respectively than FF cows. Protein percentages followed the same pattern. Fat yield was not significantly different ($p > 0.05$) between JJ and FJ cows but was lower than the yield of pure bred FF cows. Percentage milk fat and protein were highest in JJ cows and lowest in FF cows, being 4.60, 4.03, 5.30 and 3.53, 3.28, 3.85 for FJ, FF and JJ cows respectively (Table 4.1). Daily milk, fat, protein and

milksolids yields followed similar trends as total yields, except that fat and milksolids yields were not significantly different ($p>0.05$) between JJ and FJ cows.

4.4.4 Physiological factors

Parity

Parity significantly ($p<0.001$) influenced all measured milk production parameters (Table 4.1). Milk, fat and protein yield per lactation were highest in parity >4 and lowest in first parity cows. Milk yield difference between parity 3 and higher parities averaged 200 L (a 4% increase), whereas the difference between parities 1 to 3 averaged 566 L (a 16% increase). Fat and protein yield followed a similar pattern. On the other hand, log SCC declined with increasing lactation number, being significantly higher ($p<0.05$) in Parity 1 but no significant differences were detected between Parities 2, 3, and 4 and between Parities 4 and 5. Total milksolids (kg) increased from 276.9 ± 3.7 in primiparous cows to 406.6 ± 3.6 in cows with parities >4 but the rate of increase declined progressively as lactation number increased, being 17.7%, 15.3%, 4.5% and 3.6% for increases to second, third, fourth and later parities respectively. Daily milk, milksolids, fat and protein yields increased with increasing parity.

4.4.5 Environmental factors

Calving year

The effect of year of calving on the milk yield parameters of dairy cows in Tasmania is shown in Table 4.1. Milk yield was significantly different ($p<0.0001$) in all calving years, increasing with calving year except 2003, which did not follow the upward trend line and was not significantly different from the yield in 2001. Milk yield increased by an average of 2.5% between calving years except between 2000 to 2001 and 2004 to 2005 when annual increase averaged 2.9%. The percentage decline in milk yield from 2002-2003 was 2.3%. Similar trends were observed for fat and protein yields. Annual milksolids (kg) yield declined in 2002 to 2003, otherwise it increased by 21 kg in 2001 and by an average of 16 kg from 2003 to 2005. Daily yields of milk, fat, protein and milksolids increased per year except in 2003 when they declined, although yield did not differ significantly ($p>0.05$) in 2001 to 2003. Daily milk yield increased by 0.8 L from 2000 to 2001, declined by 0.3 L in 2002 to 2003 and subsequently increased by an average of 0.75 L per year.

Location

The effect of location on production traits is shown in Table 4.1. Milk, protein and milksolids yields were highest and lowest in the Far North West and King Island respectively. Production was significantly higher ($p < 0.001$) in the Far North West than the rest of the locations, but did not differ significantly ($p > 0.05$) between the Central North and North East locations. The maximum difference in milk yield/lactation among the dairying locations giving the highest yields, i.e. the Far North West, North East, Central North and North West, was 381.2 L, whereas the maximum difference between these locations and King Island was 1548.6 l. Milk fat yield was highest in the Central North and lowest in King Island and followed similar trends as milk yield. Somatic cell count was similar between cows in the different locations but was significantly lower ($p < 0.05$) in the North East and North West. Although milk, protein and fat yields were lowest in King Island, log SCC was highest in this location, being 178 ± 33.4 vs. 118.5 ± 4.8 in the North West. Total milksolids (kg) did not differ ($p > 0.05$) between the Central North and King Island. Daily milk, fat, protein and milksolids (kg) followed similar trends as observed in total yields (Table 4.1).

Calving season

Spring-calving cows, followed by winter-calving cows, produced significantly higher ($p < 0.0001$) volume of milk, and quantities of fat, protein and milksolids compared to their autumn-calving and summer-calving counterparts (Table 4.1). There were no significant ($p > 0.05$) differences between autumn and summer-calving cows in milk and component yields. Milk yield difference between spring and autumn-calving cows was 675.8 litres while fat and protein yields between cows calving in both seasons differ by approximately 25 kg. Somatic cell count (SCC) was highest in summer-calving cows and lowest in autumn-calving cows. Daily milk, fat, protein and milksolids yields followed the same trend.

Calving year x calving season interaction

There were significant effects of calving year and calving season on production (Figure 4.1). Milk and milk component yields increased and were highest in spring, and lowest in summer calving cows, irrespective of calving year except in 2002 and 2003 when autumn calving cows produced lower milksolids than cows that calved in summer.

Reduction in total milksolids, owing to the drought of 2003, in autumn and summer-calving cows, were 7.5 and 18.2 kg respectively, while spring and winter-calving cows produced 8.2 and 11.0 kg more milksolids during the same year. SCC was always highest in summer-calving cows, except in 2002, 2004 and 2005, when spring-calving cows were highest, and lowest in autumn calvers?]

Table 4.2 Least squares (\pm se) means of interaction of breed, calving year and calving season for milk, fat, protein and somatic cell count of three breeds of dairy cows.

Category	Milk (L)	Fat(kg)	Protein(kg)	Milksolids (kg)	Log SCC * $\times 10^3$	Milk (L/d)	Milksolids (kg/d)
<i>Breed x Year</i>							
Crossbred – 2000	3824 \pm 97.1	175 \pm 3.8	134 \pm 3.2	308 \pm 6.73	124 \pm 18.2	13.5 \pm 0.33	1.09 \pm 0.023
Crossbred – 2001	4095 \pm 76.7	187 \pm 3.0	143 \pm 2.5	330 \pm 5.32	109 \pm 14.4	14.5 \pm 0.26	1.16 \pm 0.018
Crossbred – 2002	4278 \pm 68.9	193 \pm 2.7	149 \pm 2.3	342 \pm 4.78	135 \pm 12.9	14.9 \pm 0.24	1.19 \pm 0.016
Crossbred – 2003	4164 \pm 62.3	194 \pm 2.4	149 \pm 2.1	343 \pm 4.79	140 \pm 11.7	14.6 \pm 0.21	1.20 \pm 0.015
Crossbred – 2004	4547 \pm 58.9	210 \pm 2.3	164 \pm 1.9	373 \pm 4.09	134 \pm 11.1	15.9 \pm 0.20	1.30 \pm 0.014
Crossbred – 2005	4609 \pm 56.1	215 \pm 2.2	165 \pm 1.9	380 \pm 3.89	167 \pm 10.5	16.1 \pm 0.19	1.32 \pm 0.013
Friesian – 2000	4801 \pm 66.2	193 \pm 2.6	153 \pm 2.2	346 \pm 4.59	131 \pm 12.4	16.8 \pm 0.23	1.21 \pm 0.016
Friesian – 2001	5147 \pm 47.7	206 \pm 1.8	167 \pm 1.6	372 \pm 3.30	120 \pm 8.9	17.9 \pm 0.16	1.30 \pm 0.016
Friesian – 2002	5197 \pm 43.2	210 \pm 1.6	168 \pm 1.4	377 \pm 2.99	124 \pm 8.11	18.1 \pm 0.15	1.31 \pm 0.010
Friesian – 2003	5109 \pm 39.2	206 \pm 1.5	169 \pm 1.3	374 \pm 2.72	133 \pm 7.3	17.9 \pm 0.13	1.30 \pm 0.009
Friesian – 2004	5397 \pm 37.7	218 \pm 1.4	181 \pm 1.2	398 \pm 2.62	136 \pm 7.07	18.8 \pm 0.13	1.39 \pm 0.009
Friesian – 2005	5619 \pm 35.2	226 \pm 1.3	188 \pm 1.1	413 \pm 2.45	155 \pm 6.6	19.5 \pm 0.12	1.44 \pm 0.008
Jersey – 2000	3550 \pm 92.2	186 \pm 3.6	134 \pm 3.0	320 \pm 6.39	109 \pm 17.3	12.5 \pm 0.32	1.12 \pm 0.022
Jersey – 2001	3655 \pm 77.7	194 \pm 3.1	141 \pm 2.6	335 \pm 5.39	119 \pm 14.5	12.9 \pm 0.27	1.18 \pm 0.019
Jersey – 2002	3742 \pm 71.	197 \pm 2.8	142 \pm 2.4	340 \pm 4.96	117 \pm 13.4	13.2 \pm 0.24	1.19 \pm 0.017
Jersey – 2003	3640 \pm 66.4	195 \pm 2.6	143 \pm 2.2	337 \pm 4.61	138 \pm 12.5	12.9 \pm 0.23	1.18 \pm 0.159
Jersey – 2004	3789 \pm 64.7	201 \pm 2.5	148 \pm 2.1	349 \pm 4.49	134 \pm 12.1	13.4 \pm 0.22	1.22 \pm 0.015
Jersey – 2005	3902 \pm 62.8	208 \pm 2.5	153 \pm 2.1	361 \pm 4.36	145 \pm 11.8	13.8 \pm 0.22	1.27 \pm 0.015
<i>Breed x Season</i>							
Crossbred – Autumn	3900 \pm 68.3	182 \pm 2.6	138 \pm 2.3	319 \pm 4.74	103 \pm 12.8	13.9 \pm 0.23	1.13 \pm 0.016
Crossbred – Spring	4764 \pm 41.4	216 \pm 1.6	168 \pm 1.4	384 \pm 2.87	141 \pm 7.8	16.6 \pm 0.14	1.35 \pm 0.009
Crossbred – Summer	3851 \pm 156.6	172 \pm 6.1	134 \pm 5.1	307 \pm 10.9	164 \pm 29.4	13.4 \pm 0.54	1.07 \pm 0.037
Crossbred – Winter	4498 \pm 38.4	213 \pm 1.5	162 \pm 1.3	374 \pm 2.66	131 \pm 7.2	15.8 \pm 0.13	1.31 \pm 0.009
Friesian – Autumn	5368 \pm 36.8	218 \pm 1.4	177 \pm 1.2	395 \pm 2.55	121 \pm 6.9	18.7 \pm 0.13	1.38 \pm 0.009
Friesian – Spring	5310 \pm 59.1	213 \pm 1.3	175 \pm 1.1	389 \pm 2.31	143 \pm 6.3	18.6 \pm 0.11	1.36 \pm 0.008
Friesian – Summer	5094 \pm 59.2	199 \pm 2.3	163 \pm 1.9	362 \pm 4.10	129 \pm 11.1	17.6 \pm 0.20	1.26 \pm 0.041
Friesian – Winter	5074 \pm 33.4	208 \pm 1.3	169 \pm 1.1	377 \pm 2.31	140 \pm 6.3	17.7 \pm 0.11	1.32 \pm 0.008
Jersey – Autumn	3014 \pm 55.9	168 \pm 2.2	117 \pm 1.8	285 \pm 3.88	113 \pm 10.5	11.1 \pm 0.19	1.02 \pm 0.013
Jersey – Spring	4235 \pm 38.9	217 \pm 1.5	161 \pm 1.3	378 \pm 2.69	133 \pm 7.3	14.6 \pm 0.13	1.31 \pm 0.009
Jersey – Summer	3802 \pm 196.7	200 \pm 7.7	147 \pm 6.5	347 \pm 13.7	144 \pm 36.9	13.5 \pm 0.67	1.20 \pm 0.047
Jersey – Winter	3800 \pm 36.5	203 \pm 1.4	148 \pm 1.2	352 \pm 2.53	117 \pm 6.9	13.4 \pm 0.13	1.23 \pm 0.009

All tested factors were significant ($P<0.0001$)

SCC= Somatic cell count

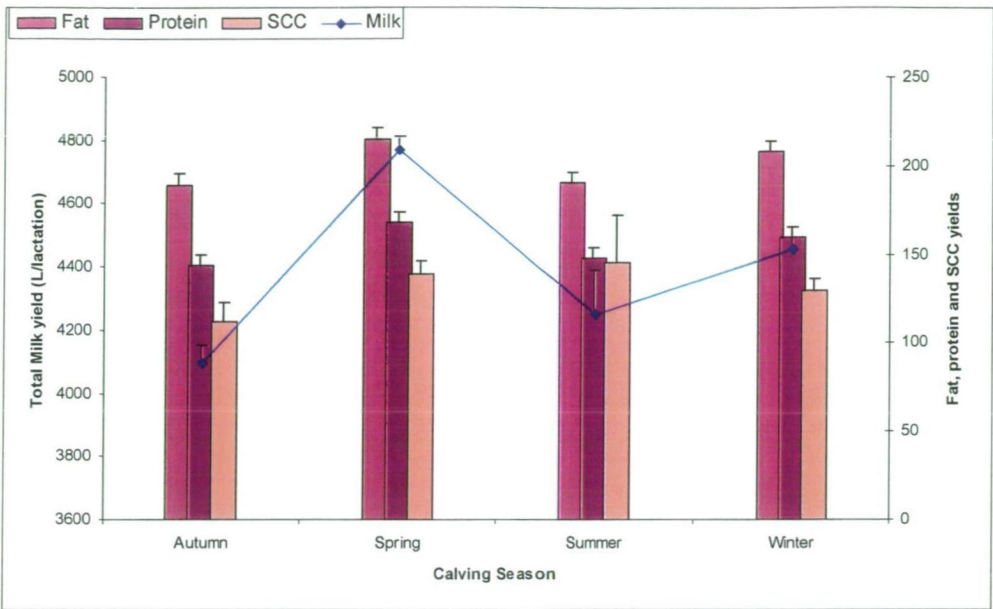


Figure 4.1. Five year mean yields of milk, fat, protein and somatic cell count (\pm se) by calving season.

4.4.6 Management factors

Herd size

Significant variation in milk production due to differences in herd size was observed between locations. Very-large herds produced the most milk, fat, protein and milksolids while medium sized herds produced the least (Table 4.1). Milk fat yield and average SCC did not differ ($p>0.05$) between medium and small herds. Cows in the small herd class had the highest SCC compared to very-large herds, which had the lowest. As with total yields, daily milk, fat, protein and milksolids were highest in the very-large herds and lowest in the medium herd class. Whereas cows in small herds produced more milk, protein and milksolids per day than their counterparts in large and medium herds, cows in large herds produced more fat per day than those in small or medium herds.

4.4.7. Genotype x environmental interaction

Breed x calving year interaction

The effect of cow breed x calving year interaction is shown in Table 4.2. Total and daily milk, fat, protein and milksolids yields increased in all the breeds with increasing calving year except in 2003, when milk, fat and milksolids yield was lower than in the preceding year. Protein yield on the other hand remained unchanged in FJ and increased in FF and JJ cows in 2003. Milk and milk constituent yields were always higher irrespective of calving year in FF cows than their JJ and FJ counterparts, while somatic cell count was generally lowest in JJ

irrespective of calving year. Milk yield (L) difference between the highest and lowest calving year for each breed were: 817.8, 785.5, and 351.8 for FF, FJ and JJ breeds respectively. Milk fat yield declined by between 2.9 and 3.8 kg in FF and JJ breeds from 2002 to 2003, but increased by 1.3 kg in FJ during the same period. Jersey cows produced more fat than FJ in 2000 to 2002, both produced equal amounts of fat in 2003 but the FJ produced more fat than Jerseys in the subsequent calving years. Of all the breeds, only the FJ produced more fat in 2003 than in 2002. Holstein-Friesian cows produced an average of 20 kg more protein irrespective of calving year than either FJ or JJ. Milk protein yield was similar between JJ and FJ breeds in 2000-2002 but the latter produced 6-15 kg more milk protein in 2003-2005. Milk protein yield was lower although not significantly ($p>0.05$) in 2002 than 2003 in all breeds except FJ. The FF breed produced milk with higher SCC in 2000-2001 than the other breeds while FJ produced milk with the highest SCC in 2002-2005.

Breed x calving season interaction

The influence of cow breed x calving season interaction on the yield of milk and constituents is shown in Table 4.2. Milk yield of FF cows were generally higher irrespective of calving season than either JJ or FJ. Holstein-Friesian breeds produced the highest level of milk and components yields in autumn as against spring in JJ and FJ breeds in all calving years. Yields of milk and components were lowest among summer-calving cows irrespective of calving year. Seasonal variation in milksolids (kg) were 33, 76.9 and 92.6 in FF, FJ, and JJ breeds respectively. Irrespective of genotype, variation in milk and component yields were lower between spring and winter-calving cows than between either of these and cows calving in other seasons. Milk fat yield was highest in autumn-calving FF and lowest in autumn-calving Jersey cows. Autumn-calving FF cows produced more milk protein than FF cows calving in other seasons, whereas spring-calving FJ and JJ produced the highest milk protein level than their counterparts calving at other seasons.

4.4.8 DATA2 Genetic Analysis

Least squares means of the production traits in FF cows obtained from fitting equation 4.2 to the data are shown in Table 4.3. Milk, fat and protein yields were highest in third and lowest in first parity cows. Log SCC values were similar across parities. Parity 3 cows produced 651L more milk at 305d than second parity cows while the latter produced 661L more milk than the first parity cows. Mean 305d milk fat and protein yields were highest in autumn calving cows. Milk yield was lowest in spring calving cows while fat and protein yields were

lowest in summer calvers. Holstein-Friesian cows calving in autumn produced 614L more milk than those that calved in winter. The latter produced 185L and 105L more milk at 305d than those calving in spring and summer respectively. Autumn calving FF cows produced 7.0% and 9.5% more total fat and protein respectively than their winter calving counterparts but the difference between summer and spring calving cows was marginal.

Milk, fat and protein yields per cow increased linearly every year from 2000 to 2005 except for a slight production dip in 2002. Average annual rate of increase in yields was 3.3%, 3.2% and 3.8% for milk fat and protein respectively. Milk and protein yield/cow were highest in the North West dairy region followed by the Far North West and lowest in King Island. On the other hand, FF cows in the Central North produced the highest quantity of milk fat followed by the North West and Far North West with cows in King Island again producing the least. The difference in milk yield/cow between the highest and the lowest producing location was 1376L although the differences between the three best producing locations averaged 188.7L. Fat and protein yields (kg/cow) differed less dramatically and ranged between 202–237 and 152 – 197 respectively. Somatic cell count varied little between parity groups, production years and locations.

Table 4.3. Least squares means of 305d milk, fat, protein and log SCC of Holstein-Friesian cows adjusted for terms in the animal model based on DATA2.

Category	Milk (L)				Fat (kg)				Protein (kg)				Log SCC				Count
Parity	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Count
1	4859	1440	1209	12997	196.6	52.88	18	509	161.6	48.65	22	469	3.83	0.976	0	8.23	18767
2	5520	1647	1247	13550	223.6	60.35	25	480	186.1	55.57	38	450	3.90	1.061	0	8.53	15677
3	6171	1746	1207	15141	250.6	66.12	27	544	207.9	57.93	16	487	4.29	1.163	0	8.94	31470
<i>Calving Season</i>																	
Winter	5648	1613	1207	14924	231.6	62.22	18	544	190.7	54.59	16	487	4.05	1.089	0	8.94	32998
Spring	5463	1825	1210	14946	219.1	66.37	25	517	182.3	60.62	34	468	4.12	1.134	0	8.53	24600
Summer	5542	1931	1296	12944	218.1	73.53	43	460	179.7	61.9	39	414	3.89	1.535	0	7.28	1230
Autumn	6262	1762	1230	15141	251.8	68.15	38	527	210.9	60.38	40	467	3.98	1.024	0	8.06	7086
<i>Calving Year</i>																	
2000	4844	1378	1229	14946	197.5	55.03	29	495	157.5	44.93	22	468	3.83	1.235	0	8.47	4385
2001	5436	1486	1474	14199	218.1	55.90	52	472	178.8	47.81	49	456	3.83	1.111	0	7.60	6639
2002	5251	1557	1247	13112	212.6	60.81	40	507	172.9	51.27	34	432	4.08	1.014	0	7.82	9024
2003	5510	1608	1230	13861	222.5	60.86	18	517	185	53.01	40	438	4.01	1.079	0	8.15	11677
2004	5816	1699	1317	14360	236.4	63.45	27	509	197.6	56.83	26	471	4.09	1.120	0	8.39	14774
2005	6024	1929	1207	15141	245.1	71.05	31	544	204.8	65.06	16	487	4.21	1.109	0.69	8.94	19415
<i>Location</i>																	
FNWest	5779	1684	1209	14924	234.6	63.73	18	544	194.9	57.44	40	487	4.02	1.068	0	8.53	17152
NWest	5897	1945	1230	15141	234.9	68.15	44	509	196.9	62.42	41	469	3.97	1.231	0	8.35	14949
CntNorth	5749	1640	1229	13929	237.0	66.52	29	514	194.3	57.19	22	435	4.13	1.082	0	8.66	12376
South	5231	1298	1273	10024	209.2	55.3	46	380	174.7	43.1	44	328	4.39	0.926	2.08	8.07	1108
NEast	5365	1631	1207	14946	216.9	62.16	27	517	179.9	55.45	16	468	4.12	1.071	0.69	8.94	18596
King Isl.	4581	1331	1210	9739	202.1	62.1	52	446	152.0	44.25	42	346	4.21	1.018	1.39	7.54	1733

SCC= Somatic cell count

Parity >2 were pooled and labelled as Parity 3

Locations = Far North West, North West, Central North, South, North East and King Island respectively.

Heritability of traits

Additive genetic and residual variance and heritability of the traits as determined with univariate analysis are shown in Table 4.4. Heritability (h^2) of 305d protein yield was lower than that of milk and fat yields which were similar. Heritability of log of somatic cell count was highest while that of protein was lowest. Table 4.5 show the result of bivariate analysis of the the traits. Phenotypic correlations ranged from 0.92 (milk vs. protein) to -0.03 for protein vs. log SCC. Phenotypic correlation between fat and protein was higher than that between milk and fat. Similarly, genetic correlation was highest between milk and protein (0.85) and lowest between fat and log SCC (0.03). Phenotypic correlations between the traits were generally higher than the genetic correlations except between milk vs. log SCC and fat vs. log SCC.

Table 4.4. Additive and residual variance and heritability (\pm se) of milk, fat, protein and log somatic cell count of Holstein-Friesian cows

Trait	Additive variance	Residual variance	Heritability
Milk	63.58	140.06	0.24(0.017)
Fat	58.64	140.52	0.26(0.016)
Protein	55.82	140.68	0.18(0.013)
Log SCC	47.69	143.69	0.32(0.009)

SCC=Somatic Cell count

Table 4.5 Heritability, phenotypic and genetic correlations (\pm se) of milk, fat, protein and log somatic cell count of Holstein-Friesian cows

Trait	Milk	Fat	Protein	Log SCC
Milk	0.41 (0.047)	0.66 (0.003)	0.92 (0.008)	-0.047 (0.004)
Fat	0.41 (0.009)	0.37 (0.005)	0.75 (0.002)	-0.05 (0.004)
Protein	0.85 (0.003)	0.61 (0.007)	0.35 (0.005)	-0.03 (0.004)
Log SCC	0.09 (0.013)	0.034 (0.013)	0.098 (0.014)	0.28 (0.005)

NB: Heritability shown in bold (diagonal), phenotypic correlation and genetic correlation on upper and lower triangles respectively.
SCC = Somatic cell count

4.5 Discussion

4.5.1 Factors affecting production traits

The model used (Equation 4.1) explained between 42-45% of the variations due to the factors tested for all traits considered in the study (Table 4.1). This would imply that there are other potentially useful explanatory variables which may not have been included in the model. This

is because a fixed model was used i.e. variations due to non-additive genetic and permanent environmental effects were not accounted for in the model. Temporary environmental factors like feed intake, feed quality, milking frequency, housing condition, diseases and other management factors are also important drivers of milk and milk constituent production in dairy cows. Detailed information about herd level management was not available in the data sets that we used in this study. Management factors due to farmer experience and openness to adoption of scientific and technological tools can have tremendous impact on productivity even when animals of similar breed and production merit have been used (Chapman *et al.* 2004). The results of this study should therefore be interpreted in the light of the available data and tested factors.

4.5.2 Genetic factors

Breed

As mentioned in the materials and method section incomplete data and missing pedigree information on some cows hampered the estimation of genetic parameters. The results of the heritability should therefore be interpreted in the light of the limitations imposed by data quality. Milk yield/lactation of FF cows reported in this study is lower compared with the performance of the North American strain reported by Horan *et al.* (2005), but is in agreement with the milk, fat and protein yields of the New Zealand strain reported in the same study. The mean pedigree index for milk yield was significantly higher for the North American strains than the New Zealand strains. Similar results as obtained in this study were also reported for pasture-based FF heifers over three lactations (Dobos *et al.* 2001). White *et al.* (2002) reported a significant breed effect for pasture-based dairy cows. In their study, Jersey cows produced 23.3% less milk than Holsteins.

Total milksolids yields obtained in this study are higher than values reported for FF cows in New Zealand (García *et al.* 1998, Lopez-Villalobos *et al.* 2001). Their study evaluated two strains of FF cows bred for low and high body weights, under low stocking rates (1.95-2.25 cows/ha) supplemented with 0.4-1.20 t DM/cow concentrate. Stocking rates in dairy farms in Australia averaged 2.5 cows/ha (Dairy Australia 2005). Poor efficiency of grain supplement utilisation due to higher level of substitution under low stocking rates or high pasture allowance has been reported in literature (Robaina *et al.* 1998, Stockdale 1999, Fulkerson *et al.* 2001). Higher daily milksolids (kg) for FF cows than found in this study was reported by

Larborde *et al.* (1998). However, their measurements were based on short duration early or mid-lactation studies, whereas we reported over the entire lactation. Similar daily milksolids yield as reported herein are in agreement with findings of Penno *et al.* (1999) and Bryant *et al.* (2003), the latter report being based on FF cows stocked at 4.4 cows/ha receiving 1.3-1.5 t DM supplement per annum for three seasons.

The higher performance of FF cows over the JJ cows demonstrated the benefit of heterosis. The rate of genetic progress in the dominant dairy breeds was evident in the annual rate of increase in milk and constituent yields. Whereas increase in milk yield/lactation averaged 5% and 5.3% in FF and FJ breeds respectively, it was only 3% in JJ. In addition, the percentage decline in lactation in 2003 was 1.7% in FF while it was 2.7% in FJ and JJ. Madgwick and Goddard (1989) had highlighted the possibility of a slower genetic progress which might make Jersey cows less competitive in the future.

4.5.3 Physiological factors

Parity

Milk production increases with parity and cow age due to increased body weight, larger capacity for dry matter intake, increase in size of the udder and recurrence of pregnancy and lactations (Capuco *et al.* 2001). Lower production in primiparous cows is related to competition between tissues (e.g. mammary gland vs.. peripheral tissues) for metabolites for growth and lactation in the immature animal (Radcliff *et al.* 2000). The effect of parity on the performance of dairy cows has been reported extensively in the literature (Tozer and Huffaker 1999, Val-Arreola *et al.* 2004). The lower incidence of somatic cell count in the milk of lower compared with higher parity cows may be attributed to the improved management practices (hygiene) and early detection (automatic detection of cell count in daily milk) and possible culling of cows with high cell count from the herd.

4.5.4 Environmental factors

Calving year, calving season and interactions:

Total yields of milk, fat and protein in this study (Table 4.1) were higher than values reported for low and high body weight Holstein-Friesian cows in New-Zealand (García *et al.* 1998, Lopez-Villalobos *et al.* 2001), and lower than the values reported by Bargo *et al.* (2002) and Garcia *et al.* (2007) for high merit cows on pasture allowance and concentrate

supplementation and individual vs. group feeding trials respectively. However, our results on total milk yield per lactation are in agreement with the findings of Grainger and Mathews (1989) and García and Holmes (2001). The latter reported milk yield of 4982-5409L, s.e. = 85.7 in autumn and spring-calving FF cows. Higher responses in milk and component yields under experimental conditions compared with aggregate data emanating from large number of cows from multiple herds over diverse locations are not unexpected. For instance, in the studies by Bargo *et al.* (2002) and Garcia *et al.* (2007), grazing cows were offered concentrate at 1kg/4kg milk yield and 3-7kg as fed/cow/d, utilising twenty-four and fifty cows respectively, whereas we evaluated data on 130,366 cows. Studies on annual increase in milk yield in this study was generally lower than the national averages (Dairy Outlook 2006, DPIW 2005) but annual milk yields in 2000 to 2001 and 2003 to 2004 (Table 4.1) are well in agreement with the reported figures. The restriction of our data sets to production records of only three genotypes might account for the discrepancy with the national figures. Further, differences in milk yield per cow due to higher use of concentrate feeds in the states of Victoria and New South Wales (Dairy Outlook 2006) may also partly explain the lower milk and component yields in Tasmania. The decline in production in the 2002/03 calving season was attributed to feed shortage from the severe and widespread drought of that season. Climatic factors such as low rainfall and adverse temperature have a negative effect on milk yield in temperate cows through the physiologically induced depressed feed intake (Walter 2006). Analysed climatic data (SILO 2008) showed that the maximum temperature was significantly lower ($p<0.05$) in 2004 than other years while mean annual rainfall was 612.2 ± 33.9 mm in the 2002/03 calving season compared with 780.4 mm for other years. Reduced rainfall could depress pasture dry matter (DM) yield and metabolisable energy (ME) content thereby reducing energy intake and productivity of pasture-based cows (Walker *et al.* 2004). Differences in milk yield between calving years have been reported (Dairy Australia 2005, Msanga *et al.* 2000). Unlike in this study, White *et al.* (2002) found no significant interactions between calving season and other factors.

Our results are also in agreement with seasonal variation in milk and milksolids yields reported by García *et al.* (1998) for pasture-based cows. They reported that autumn-calving FF cows produced significantly more milksolids than spring-calving FF cows due to the effect of lush pasture with higher ME in spring (spring hump) and extended lactation due to greater persistency. Typically, dairy cows attain peak yields between 3-8 weeks postpartum (Tekerli *et al.* 2000). In pasture-based winter calving systems, cows' peak month of

production coincide with spring, i.e. October, when production almost doubled that of the lowest months in May-July. Although we did not evaluate yield by lactation stage, our findings revealed that lactation length was significantly longer ($p<0.05$) in autumn-calving, compared with spring-calving FF cows (305.9 ± 0.34 vs. 269.11 ± 0.16). On the other hand, White *et al.* (2002) reported that autumn and spring-calving cows had similar milksolids yields in northern Victoria. Differences in production traits during different calving seasons reflects seasonal calving systems practiced all over Australia aimed at minimising feed cost by matching the peak in nutrient requirement for lactation with the period of highest availability of ME from pasture (Doyle and Kelly 1998, Walker *et al.* 2004). Although most farms practice a split calving system, the percentage calving pattern of dairy herds in Tasmania were 51% and 38% for winter and spring calving respectively.

Location

Milk yield per cow in the 2002/03 calving season obtained in this study was higher than reported averages in other states of Australia except Western and South Australia. Production per cow in Tasmania was lower than that of other states except Queensland in 2003/04 (Dairy Australia 2005). Differences in yield traits between locations, attributable to differences in the rainfall distribution pattern and geo-physical conditions, have been reported extensively in the literature (Msanga *et al.* 2000, Horan *et al.* 2005, Dairy Australia 2005). A review of climate data in the study area showed that mean annual rainfall and altitude were significantly different ($p<0.001$) between the dairying locations in Tasmania. Mean annual rainfall was lower in the South but significantly higher ($p<0.01$) in King Island compared to the other locations. Mean altitude (meters above sea level) averaged 117.7 ± 16.4 m in the Central North, North West, North East and Far North West locations compared with an average of 43.6m in the South and King Island. (SILO 2008). In addition, considerable investment undertaken in the North West and North East areas of the state in the last decade has encouraged the emergence of corporate farmers with large herds employing improved production systems (DPIW 2005). It should be noted, however, that the relatively smaller number of cows (Table 4.1) in the South and King Island could bias some of the responses evaluated in these locations.

4.5.5 Management factors

Herd size

Herd sizes reported in this study are generally consistent with the national dairy herd statistics (Dairy Outlook 2006). Tasmania has the highest mean herd size of 254 cows per herd, while Queensland has the smallest with 158 cows per herd. Higher performance in herds with large number of cows is also in agreement with results from dairying in Victoria. A benchmark study in Western Victoria that compared profitability indices of the top and bottom 10 farms indicated that large herds were more profitable and gave greater returns on capital than medium or small herds. As herd size increases, overhead and labour costs can be spread over more units (Doyle and Kelly 1998). In addition, owners of larger herds are reported to adopt high intensity feeding systems and are more open to improved management systems than small or medium herd owners (DRDC 1996). Smaller herds, on the other hand can benefit from the flexibility in land and labour management to increase per unit resource (Doyle and Kelly 1998).

4.5.6 Heritability of milk, fat and protein yields.

The relatively small size of the data sets used in this study could bias the heritability (h^2) estimates. The greater the sample size, the higher the precision of additive genetic estimates (Swalve 2000, Jensen 2001, Schaeffer 2004). The h^2 estimated using both univariate and multivariate approaches are within the range of values reported in the literature which ranged from 0.31 (Wilmink 1987, Rekaya *et al.* 1995) to 0.49 (Pander *et al.* 1992). Meyer *et al.* (1989) compared the different methods of estimating h^2 and reported a 305d milk yield h^2 of 0.37. In a study comparing alternative methods of equalizing heterogeneity of variance Boldman and Freeman (1990) reported lower h^2 of milk for untransformed yield in low, medium, and high producing herds to be .18, .22, and .24. Heritability of fat and protein reported in this study are higher than the values reported by Vissher and Goddard (1995) from five states of Australia excluding Tasmania. They used test-day sire models in their evaluation while we utilised an animal model with 305d records, although the sample sizes were similar for both studies. Our results are also in agreement with the work of Swalve (1995) who utilised a test-day, herd-year-season animal model and reported 305d milk, fat and protein h^2 to be 0.39, 0.32 and 0.30 respectively.

Comparison of h^2 estimation methods showed that test-day approaches generally yield lower and more precise estimates (Wilmink 1987, Meyer *et al.* 1989, Pander *et al.* 1992, Reents *et al.* 1994) compared with the 305d method. Issues resulting from using aggregated 305d milk yield and the benefits of test-day random regression models have been extensively reviewed

(Swalve 2000, Jensen 2001 and Schaeffer 2004). The use of 305d milk yield stems from industry tradition and the limitations imposed by computational requirements until recently (Jensen 2001, Schaeffer 2004). However, there is a general consensus that the heritabilities for fat were, in almost all cases, lower than the heritabilities for protein, and that milk production has the highest heritability.

4.6 Conclusions:

This study set out to investigate the influence of genetic, physiological and herd management factors affecting dairy production in Tasmania. Breed, parity, age and lactation length are important determinants of milk and milksolids yields under pasture-based dairy systems. Improving yields over the years are indicative of improvement in dairy cow genetics but also in adoption of better management practices. Production in Tasmania is seasonal with spring calving cows generally outperforming cows calving in other seasons. The inclusion of a random cow effect in the animal model showed higher yields attributable to additive genetic variance in the FF cows, although small data sizes preclude the estimation of the additive genetic effects in the other breeds. Incomplete data and missing pedigree information limited the amount of available data and therefore the precision of heritability estimates. However, higher milk and constituent yields in the persistency of FF cows, resulting in higher milk and constituent yields of autumn-calving Holstein-Friesian cows, suggests that a 365-day calving interval would depress the yield potential of this breed. Herd size as a factor of management improved production traits in very large herds thus supports the emerging trends for larger dairy herds. Other management factors such as access to information and market, favourable market prices, and technical and managerial support, are very important if farmers are to cope with the challenge of running profitable dairy enterprises. Larger, more detailed data sizes will be required to validate the heritability estimates and elucidate the management factors affecting production at various lactation stages.

Appendix .4.1: Dairy Farm Facts in Tasmania

Parameter/Year	99/00	00/01	01/02	02/03	03/04	04/05	05/06
Milk production, million litres	609	590	671	585	590	600	622
Registered Dairy farms, nos.	734	638	612	597	543	507	498p
Dairy cow numbers, '000	139	148	134	142	138	135	135
Employment; owners and staff, nos.	1,890	NA	NA	1,700	NA	NA	NA
Gross value of production, \$M	133	148	220	151	160	180p	NA
Average herd size, cows	194	231	236	213	245	271	270
Milk per cow, litres	4,381	4,177	4,646	4,304	4,219	4,497	4542
Milk per farm, '000 litres	830	925	1,116	980	1,089	1,183	NA
Milk fat (%)	4.29	4.26	4.28	4.26	4.32	4.28	4.29
Milk protein (%)	3.29	3.28	3.29	3.29	3.36	3.36	3.37

Adapted from: Dairy Outlook 2006, p=predicted, NA=Not available

Chapter 5. Comparative effects of ASI and APR sire breeding index on the lactation profile of pasture-based Holstein-Friesian cows

5.1 Summary

Having determined that both genetic and non-genetic factors influence production traits of pasture-based dairy cows in Tasmania, this chapter evaluates the effect of contemporary changes in methods of estimating sire breeding values on the shape of the lactation curve. This will further elucidate the influence of genetic factors on production traits. Estimated Breeding Values (EBV) are useful indicators of the ability of bulls to transmit desirable traits to their progeny. The lactation profile differs between cows of different genetic merit but for pasture-based production systems, the impact of emerging EBV evaluation methods remains largely unpublished. In this chapter, Wood's incomplete gamma (IG) model ($Y(t)=at^be^{-ct}$) was utilised to compare the effects of the Australian Selection Index (ASI) and Australian Profit Ranking (APR) EBVs on the shape of the lactation profile of pasture-based dairy cows. None of the lactation parameters were significantly influenced by EBV choice. It was concluded that the IG function adequately modelled the lactation profile of a herd of cows, explaining about 90% of the observed variation irrespective of using ASI or APR sire breeding index.

5.2 Introduction

Knowledge of a breeding bull's genetic merit for dairy traits is central to improved milk production and profitability. Estimated Breeding Values (EBVs) are predictions of an animal's genetic merit, based on available performance data on the individual and its contemporaries within the same herd. In the calculation of EBVs, comparative evaluation of individual animals within each herd, or contemporary group, to the average of other animals of the same sex and age group in that herd, subjected to similar treatments under the same conditions are done using appropriate statistical tools. The pedigree links between groups are used in comparing animals of the same age group or sex that have been reared under different herds, years and management conditions.

Previously, breeding objectives focused mainly on milk production traits (Miglior *et al.* 2005), which led to fertility decline (Royal *et al.* 2002). Consequently, breeding objectives were changed to include survival and longevity traits (Buckley *et al.* 2003). Until 2001, the Australian Selection Index (ASI) based on production traits was used as the index of choice for ranking breeding bulls. The benefit of having high producing cows is reduced if they break down prematurely due to illness arising from production stress or have to be culled because of undesirable traits such as poor behaviour, slow milking speed, high cell count or low fertility. Stakeholders demand led to developing an alternative index, the Australian Profit Ranking (APR), the aim of which was to maximise profit from genetic gain (ADHIS 2001).

Mathematical models are used as tools, to elucidate the underlying biological features of lactation, in the presence of environmental perturbations (Wood 1967, Wilmink, 1987), for genetic evaluations and farm management decisions. Milk production is higher in high genetic compared with low and medium genetic merit cows (Snijders *et al.* (2001). Although Shalloo *et al.* (2004) assessed the economic impact of cow genetic potential for milk production and concentrate supplementation on the profitability of pasture-based systems and Miglior *et al.* (2005) reviewed selection indices in Holstein cattle in various countries there has been little information on the implication of emerging selection methods on lactation curves shapes. Freeze and Richards (1992), Tozer and Huffaker (1999), Horan *et al.* (2005) and Roche *et al.* (2006) have demonstrated the effect of genetic merit, breed, parity, season, nutrition, and pregnancy on the shape of the lactation curve but an important question that remains largely unanswered is: what impact does the inclusion of temperament and longevity traits in the EBV have on the lactation pattern of pasture-based cows? This chapter attempted to answer this question by examining the lactation curve parameters of pasture-based Holstein-Friesian cows selected on the basis of ASI or APR. The second objective attempts to evaluate the accuracy and reliability of the incomplete gamma (IG) function to adequately predict the lactation curves based on ASI and APR. Such information will help farmers make more informed genetic and management decisions.

5.3 Materials and methods

Lactation records (57,735, from 1968 lactations) of multiparous Holstein-Friesian cows at the Elliott Research and Demonstration Station (ERDS), Tasmania, collected from 1994-2005, were edited to exclude cows with parities >5, or with lactation length <100 or >350 days, or having less than seven test date records, leaving a total of 50,978 records (1603 lactations). The data were first divided into two sets according to production years before and after 2001, henceforth referred to as DATA1 and DATA2 to compare the parameters of the incomplete gamma (IG) model (Wood 1967) between the years preceding and after the implementation of the APR. Subsequently, analysis was performed on DATA2. The study data also included cow and sire ID, calving date, calving season and calving year. Individual cows grazed on Perennial Ryegrass *Lolium perene* on dry land or irrigated pasture in the year 2003. Three groups, viz. Parity 1, Parity 2 and Parity 3-5 (labelled herein as Parity 3), were formed. Sire ASI and APR index were obtained from the Australian Dairy Herd Improvement Scheme (ADHIS) database for May 2006.

The formulae were:

$$\text{ASI} = 3.8 * \text{Protein ABV} + 0.9 * \text{Fat ABV} - 0.048 * \text{Milk ABV} \quad 5.1$$

and

$$\begin{aligned} \text{APR} = & 3.8 * \text{Protein ABV} + 0.9 * \text{Fat ABV} - 0.048 * \text{Milk ABV} + 3.9 * \text{Survival Index} \\ & + 1.2 * \text{Milking Speed ABV} + 2.0 * \text{Temperament} \quad 5.2 \end{aligned}$$

In both EBV methods (ASI and APR), cows (DATA2) sired by bulls with $\text{EBV} \geq 20$, corresponding to the top 2% of the national bull ranking, were classified as high merit (HM), otherwise as low merit (LM). The summary statistics cow age, daily milk yield, ASI and APR indices and milk EBV are shown on Table 5.1.

Table 5.1. Summary statistics of milk yield and sire breeding index of Holstein-Friesian cows in different parity groups.

*Year	Parity	Variable	Mean	Min	Max	Stdev	N [§]
DATA1 ⁺	1	Age	24.5	22.5	29.1	1.08	10201
		Milk EBV	37.3	-1152	992.0	310.0	8707
		ASI index	-4.8	-106.0	48.0	26.30	8707
		Milk yield	14.6	1.00	30.4	4.63	10195
	2	Age	36.9	34.3	41.2	1.14	8289
		Milk EBV	-6.0	-991	992.0	313.96	6873
		ASI index	-9.4	-70.0	46.0	25.89	6873
		Milk yield	16.5	1.0	36.5	5.61	8285
	3	Age	59.2	46.9	77.8	9.68	16875
		Milk EBV	-93.2	-1121	672	369.2	14380
		ASI index	-9.4	-70.0	46.0	25.89	14380
		Milk yield	16.5	1.0	36.5	5.61	16862
DATA2 [†]	1	Age	24.3	23.1	26.1	0.63	3668
		Milk EBV	193	-753	917	373.8	3606
		APR index	14.5	-66.0	80.0	36.3	3606
		Milk yield	14.9	1.4	41.4	4.49	3667
	2	Age	36.8	35.2	38.6	0.72	3086
		Milk EBV	163	-1152	917	388	3024
		APR index	10.4	-159	80.0	43.6	3024
		Milk yield	17.1	2.4	42.7	5.23	3084
	3	Age	61.1	47.3	74.8	9.75	8785
		Milk EBV	103	-1152	922	337	7509
		APR index	2.2	-159.0	80.0	39.2	7509
		Milk yield	19.6	1.0	49.7	6.38	8785

* Year=Production year ; ⁺DATA1=Data from 1994 to 2000, [†]DATA2=Data from 2001 to 2003; Parities >2 were pooled and labeled as Parity 3, § N = Number of observations.

5.3.2 Statistical Analysis

The incomplete gamma function (Wood 1967) was used in fitting the lactation curve and was defined as

$$y(t) = at^b e^{-ct} \quad 5.3$$

where $y(t)$ is the average daily milk production at time t (weeks), a is a scaling factor to represent yield at the beginning of lactation, b and c are factors associated with the inclining and declining slopes, respectively, of the lactation curve. Data were analysed using the Marquardt's iterative method of the non-linear (PROC NLIN) procedure of SAS (SAS 2002) on lactation stage defined as week in milk (WIM) for the various herds (DATA1) while actual test-day milk yield were used for individual cow's (DATA2) analysis. Estimates of least squares means for week in milk (WIM) were computed using PROC GLM (SAS 2002) to fit herd data while WIM and milk yields from actual test dates were used for individual curve fits. Model parameter estimates were compared for significance within parity groups and EBV class using the standard error of the difference of the mean of each identical group, i.e. cow parities were compared within each EBV type (APR and ASI) and class (high and low). The magnitude and distribution of the residuals, the root mean square error (RMSE) values of the model and the correlation between actual and predicted milk yields were further used to examine the goodness of fit of the model. Other parameters estimated from the IG models for both data sets were as follows:

$$\text{Lactation persistency } p \text{ as } p = -(b+1) * \ln(c) \quad 5.4$$

$$\text{Time to peak yield } t_m \text{ as } t_m = b/c \quad 5.5$$

and

$$\text{Peak yield } y_{max} \text{ as } y_{max} = a (b/c)^b e^{-b} \quad 5.6$$

The values obtained from t_m were multiplied by 7 to obtain the equivalent day at peak milk yield (Table 5.2). The relationship among parameter estimates of individual cows was further examined with the correlation procedure of SAS (SAS 2002) using DATA2.

5.4 Results

5.4.1 Lactation curves of parity groups (DATA1 and DATA2)

Except for first parity cows, the initial milk yield value was significantly ($P<0.05$) influenced between production years, while the incline and decline rates were also significantly different ($P<0.05$), parity group notwithstanding (Table 5.2). Lactation persistency was similar between production years. Cows selected on ASI basis (pre 2001) tended to peak later at significantly higher ($P<0.05$) levels, except for second parity cows, and produced significantly less total milk yield than those selected on APR basis.

The goodness of fit of the model as determined by the root mean square error (RMSE) indicated a good fit to the herd data (Table 5.2). RMSE ranged from 0.53–0.64 and 0.64–1.67 for pre and post 2001 cows, respectively. All the parameter estimates were significant ($P<0.01$) but the residuals were positively autocorrelated. Predicted lactation curves of parities 1-3 cows with the curve of actual milk yield of first parity cows superimposed on the predicted curve (parity 1 only) are shown in Figure 5.1. Irrespective of EBV or parity group, the IG model over-predicted initial and mid lactation milk yield, while under-predicting yield in late lactation, although the error of prediction was higher in the cows sired by bulls selected on APR compared with those selected on ASI basis (see parity 1 predicted and actual curves). The margin of prediction error declined as lactation progressed until around mid-lactation (week 22-25) and towards the end of lactation when it increased again. Residuals of predicted milk yield (L) ranged from -2.3–2.6 and -2.5–3.6 in DATA1 and DATA2, respectively. The correlation between observed and predicted values averaged 0.96 irrespective of EBV level and parity group.

Table 5.2. Lactation parameter estimates and root mean square error of pre and post 2001 Friesian cows modeled with the IG model.

Estimates (\pm se) of lactation curve ¹ parameters								
DATA	Parity	<i>a</i>	<i>b</i>	<i>c</i>	Persis- tency ²	Pkday ³	Pkyd ⁴	RMSE ⁵
1	1	16.8(0.54)	0.14(0.025)	0.03(0.002)	4.00	33	18.1	0.62
2	1	17.0(0.55)	0.07(0.020)	0.02 (0.001)	4.19	25	17.3	0.64
1	2	21.0(0.57)	0.13(0.022)	0.03 (0.002)	3.96	30	22.3	0.64
2	2	22.4(0.92)	0.002(0.026)	0.02 (0.002)	3.92	1	22.3	1.67
1	3	24.0(0.52)	0.19(0.023)	0.04 (0.001)	3.83	33	26.8	0.53
2	3	26.0(1.74)	0.08(0.023)	0.03 (0.002)	3.79	19	25.9	1.67
SED		0.80	0.023	0.002				

¹Lactation parameters of IG models ($y(t) = at^b e^{-ct}$) are a =initial milk yield, b =incline phase, c =decline phase

²Persistency, calculated as $s = -(b+1)\ln(c)$.

³Pkday=Day at peak, t_m as $t_m = b/c$

⁴Pkyd=milk yield at peak, calculated as $y_{max} = a(b/c)^b e^{-b}$

⁵RMSE=Root mean square error

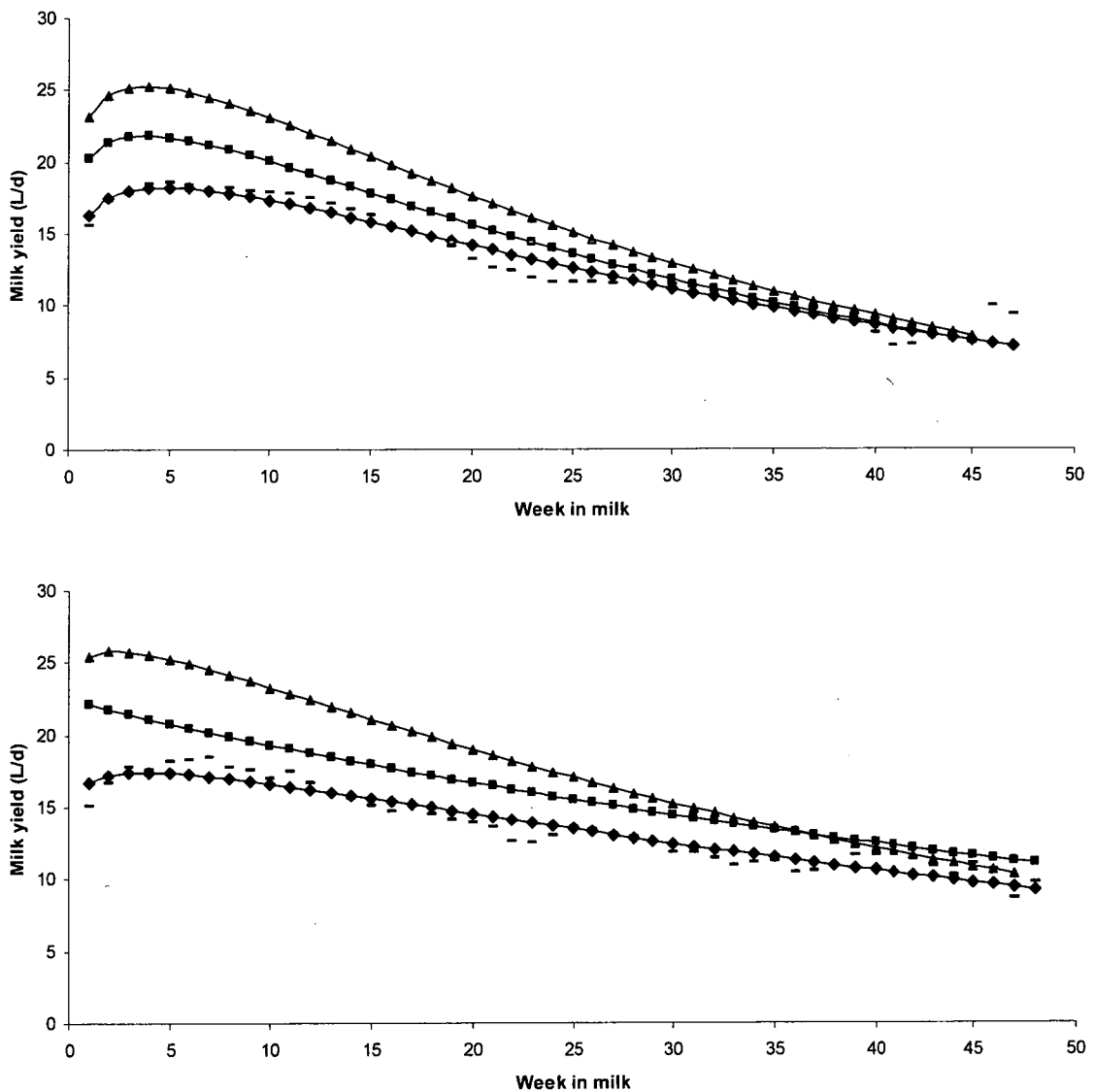


Fig 5.1. Predicted milk yield curves of dairy cows prior to and after the introduction of Australia Profit ranking (APR).

Curves are top = Pre APR production years and bottom = Post APR production years and parity1 (diamonds), actual milk yield parity1 (dashed line) superimposed on predicted milk yield, parity2 (squares) and parity3 (triangles).

5.4.2 Lactation curves of individual cows

The accuracy of prediction of daily milk yield as determined by the root mean square error values was lower in individual cows (DATA2) compared with parity groups (Table 5.4). None of the individual cow's lactation data had RMSE <1. However, the percentage of lactation data fitted with RMSE <5 averaged 81.9 and 88.1 for cows selected on the basis of APR and ASI respectively. Root mean square error values averaged 4.54 and 4.58 for first and second parity HM cows while it averaged 4.30 and 4.79 for first and second parity LM cows. Mean parameter estimates with standard errors are shown on Table 5.4. None of the parameters of the IG model or the derived parameters was significantly influenced by EBV selection method. The percentage of cows exhibiting the non-standard curve shapes, i.e. a decline followed by a rise (reverse standard) or a continuously declining curve type, did not differ within EBV level although the proportion were higher among HM cows, being approximately 14% compared with 7% for LM cows (Table 5.4). The three main types of curve shapes of individual cows detected by the IG model are shown in Figure 5.2.

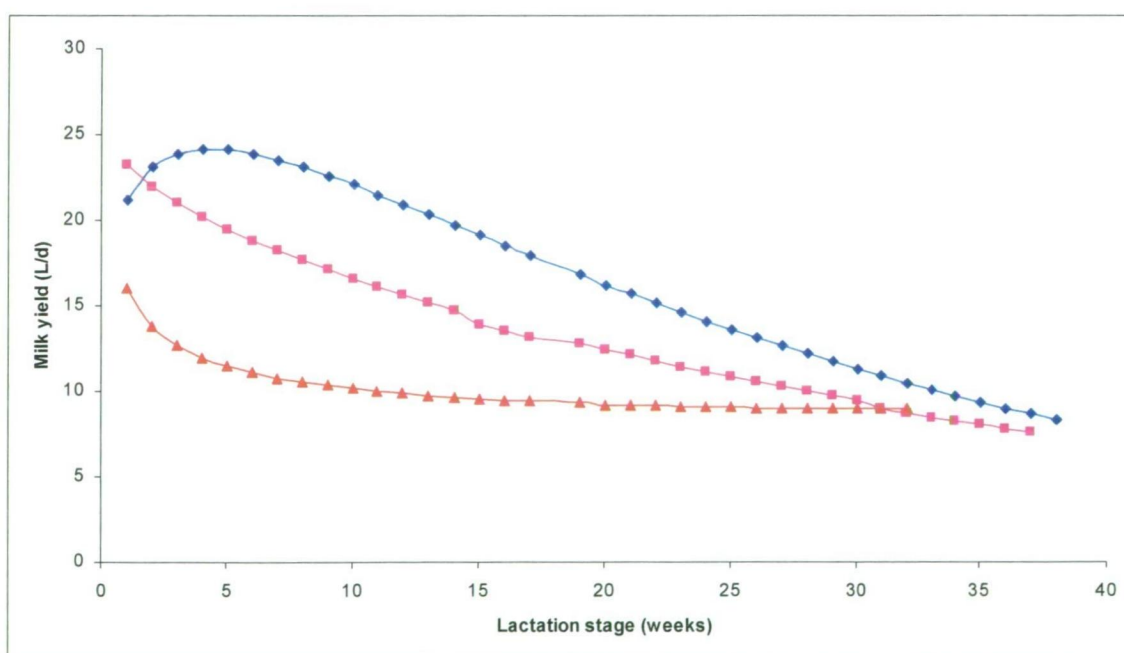


Fig 5.2. Different lactation curve shapes of individual cows detected by fitting pasture-based lactation data to the IG model.

Curves are \triangle $b=-0.22$ $c=-0.006$, \square $b=-0.05$ $c=0.03$, and \diamond $b=0.18$ $c=0.04$. Curve shapes are, respectively, \triangle non-standard or reverse standard (=a decline to a nadir followed by an incline), \square continuously declining, and \diamond standard = an incline to an apex followed by a decline.

Partial correlation coefficients among lactation parameter estimates are shown on Table 5.5. In HM cows selected on the basis of APR, the EBV indices (Production APR, ASI index and Milk EBV) were weakly correlated with all the parameter estimates of the IG model, being an average of -4.9%, 10.5% and 3.5% respectively. Parameter a was also weakly correlated with parameters b and c but highly correlated with lactation persistency, peak and total milk yields. The rate of incline was highly correlated with the decline rate and total milk yield, although the correlation with persistency and peak milk yield was not as strong. Similarly, the decline rate was also poorly correlated with peak milk yield while peak yield was fairly well correlated with total milk yield. Of the three EBV indices, the production, APR and ASI indices were strongly correlated, otherwise the correlation was moderate.

Similar relationships among the correlation coefficients were found between the EBV indices of LM cows as those of the HM group. All the indices are weakly but negatively correlated with the IG parameter estimates except the correlation between milk EBV and total milk yield, which was positive. Compared with the HM group, the correlation between Wood's IG model parameters a , b and c in the LM group are higher, except for that between parameters a and c , a and peak milk yield, b and c and b and peak milk yield.

Table 5.3. Frequencies and percentage of different curve shapes of individual cow's lactation data detected by the IG model.

EBV	Level	No Obs	% obs	Parameters		Curve shapes
				b	c	
APR	High	283	85.8	+	+	Standard lactation curve
		46	13.9	-	+	Reverse standard curve
		1	0.3	-	-	Continuously decreasing
ASI		208	85.2	+	+	Standard lactation curve
		35	14.3	-	+	Reverse standard curve
		1	0.4	-	-	Continuously decreasing
APR	Low	971	93.0	+	+	Standard lactation curve
		71	6.8	-	+	Reverse standard curve
		2	0.2	-	-	Continuously decreasing
ASI		1048	92.8	+	+	Standard lactation curve
		79	7.0	-	+	Reverse standard curve
		2	0.2	-	-	Continuously decreasing

Table 5.4. Mean parameter estimates of individual cow lactation parameter estimates (\pm se) of post 2001 Friesian cows modeled with the IG model.

EBV method			Estimates			
Level			High (n=17)		Low (n=11)	
EBV	Parity	Parameter	Mean	se	Mean	se
APR	1	a	16.3	0.75	17.0	1.38
		b	0.26	0.029	0.18	0.051
		c	0.04	0.005	0.03	0.004
		Persistency	4.08	0.109	4.18	0.092
		Pkday	46.3	4.35	37.0	7.51
		Pkyd	20.2	0.45	19.7	0.63
		Totmlk	4591	251	4674	155
		RMSE	4.86		4.40	
ASI	1		High (n=12)		Low (n=16)	
		Parameter	Mean	se	Mean	se
		a	16.2	0.77	16.8	1.09
		b	0.24	0.034	0.22	0.041
		c	0.04	0.005	0.04	0.006
		Persistency	4.15	0.096	4.10	0.112
		Pkday	46.4	5.34	39.8	5.73
		Pkyd	20.1	0.58	19.9	0.48
APR	2	Totmlk	4761	183	4521	250
		RMSE	3.93		4.89	
			High (n=12)		Low (n=8)	
		Parameter	Mean	se	Mean	se
		a	23.9	1.44	20.2	2.08
		b	0.11	0.024	0.16	0.042
		c	0.03	0.003	0.03	0.004
		Persistency	3.94	0.080	4.15	0.135
ASI	2	Pkday	24.5	4.78	36.8	8.17
		Pkyd	24.9	0.96	22.0	1.42
		Totmlk	5472	261	4892	590
		RMSE	4.22		4.76	
			High (n=11)		Low (n=9)	
		Parameter	Mean	se	Mean	se
		a	23.2	1.55	21.3	2.07
		b	0.13	0.028	0.13	0.04
c	0.03	0.004	0.03	0.002		
Persistency	3.93	0.90	4.13	0.117		
Pkday	26.2	5.19	33.4	7.69		
Pkyd	25.6	5.19	22.8	1.44		
Totmlk	5178	375	5317	450		
RMSE	4.60		4.70			

¹Lactation parameters of IG models ($y(t) = at^b e^{-ct}$) are a =initial milk yield, b =incline phase, c =decline phase

²Persistency calculated as $s = -(b + 1)\ln(c)$

³Pkday=Day at peak, t_m as $t_m = b/c$

⁴Pkyd=milk yield at peak, calculated as $y_{max} = a(b/c)^b e^{-b}$

⁵ RMSE=Root mean square error

Table 5.5. Partial correlation coefficients (x 10-2) and significance level between EBV index and lactation model parameters estimates of individual high merit APR (upper diagonal) and low merit APR (lower diagonal) cows (n=330 and 1041 respectively).

EBV Parameter ¹	Prod APR	ASI Index	Milk EBV	High merit			Persis- tency ²	Peak yield ³	Total milk ⁴
				<i>a</i>	<i>b</i>	<i>c</i>			
Prod APR		73***	-28***	-5.4	1.9	0.59	6.7	-8.1	-6.9
ASI Index	85***		-5.5	-13*	2.1	-2.9	14*	-20**	-11*
Milk EBV	36***	38***		2.9	-5.1	-6.9	1.6	0.33	1.5
<i>a</i>	2.2	3.0	1.4		-7.0***	-4.0	-50***	88***	58***
<i>b</i>	-4.8	-4.9	-4.7	-65***		93***	22***	-29***	43***
<i>c</i>	-3.2	-3.7	-8.8**	-33***	80***		-32***	-0.5	-52***
Persistence	-3.2	-3.4	7.7*	-57***	38***	-22***		-51***	13*
Peak yield	-4.9	-4.3	-2.7	79***	-11***	14***	-43***		59***
Total milk	-1.6	-0.3	1.4	52***	-21***	-30***	7.0*	65***	

Prod APR= APR production EBV value, ASI Index= ASI EBV value and Milk EBV=Milk EBV value (all obtained from ADHIS database of breeding bulls EBV)

¹Lactation parameters of IG model $y(t)=a t^b e^{-ct}$ are a =initial milk yield, b =incline rate, c =decline rate

²Persistence calculated as $s = -(b+1)\ln(c)$

³Pkyd=milk yield at peak, calculated as $Y_{max}=a(b/c)^b e^{-b}$

⁴Total milk = actual total milk yield

Significance levels are *=(P<0.05), **=(P<0.01) and ***=(P<0.001)

5.5 Discussion

5.5.1 Herd Lactation

The study of lactation curve shape is a vital tool in understanding the pattern of milk production in individual cows or herds and provides valuable information about the biological and economic efficiency of the dairy system (Grossman and Koops 1988, Schaeffer *et al.* 2000, Tekerli *et al.* 2000). This chapter used the IG model proposed by Wood (1967) to fit sample lactation data from Elliot Research and Demonstration Station (ERDS) with the objective of evaluating the effect of sire EBV method, either the ASI or APR breeding index, on the shape of the lactation curves of pasture-based cows. The second objective was to determine the usefulness of the IG model in adequately fitting lactation data from pasture-based dairy systems. The null hypothesis being tested was that the inclusion of survival, milking speed and temperament in the APR breeding value index would have no effect on the shape of the lactation curve. Previous studies had suggested that the exclusion of such traits in breeding value estimation had produced cows that were

prone to stress, especially from high peak yields followed by a sharp decline in early lactation (Teklerli *et al.* 2000, Royal *et al.* 2002, Buckley *et al.* 2003, Miglior *et al.* 2005).

The incidence of high peak yields followed by sharp declines observed in the herd data, especially in the pre-2001 cows selected on the basis of ASI (Table 5.2 and Figure 5.1), is consistent with previous reports (Horan *et al.* 2005 and Roche *et al.* 2006) that due to previous emphasis on breeding for increased milk yield, high genetic merit cows are prone to lactation with faster rise to peak yield and sharper post peak decline rate than low merit cows. Milk production of dairy cows has increased substantially worldwide in the last two decades. For example, in the United States, milk production has risen from an average of 3,173 kg/cow in 1958–1962 to 8,879 kg/cow in 2005 (USDA, 1964, 2006). Similarly, in the United Kingdom, milk production/cow increased from 3,000 kg/cow in the fifties to 6,500 kg/cow at present (Colman *et al.* 2004). During the same period, average milk production per cow in Australia increased from 2,889 kg/cow in 1980 to 5,037 kg/cow in 2005 (Dairy Outlook, 2006).

However, the differences in the production and lactation curve shapes between pre and post 2001 cows can also be attributed to the more accurate genetic evaluation system adopted in Australia with the use of the best linear unbiased prediction (BLUP) method to estimate breeding values (Fulkerson *et al.* 2008). In addition, there has been considerable improvement in management practices; especially the increase in the proportion of high energy concentrates in the diets of dairy cows, which has substantially increased milk yield in HM cows (FAO 2007). In the major dairy state of Victoria, the proportion of concentrates fed has increased from almost zero in the early 1980s to over 1.5 t/cow per yr in 2002 (Fulkerson and Doyle 2001). Also the pooling of parity >3 into one group might have some effect of increasing the error bias.

The values of initial milk yield reported in this study are higher than the values reported for cows showing the *typical* (standard) curve shape but lower than the values reported for cows exhibiting the *atypical* (non-standard) lactations (Rekik and Ben Gara 2004). The rate of incline observed in this study is in agreement, although the decline rate reported here is

lower compared with the values reported by those same authors. Similar reports as obtained with initial, rate of incline and decline, peak and total milk yields in this study have been reported by Tozer and Huffaker (1999) and Val Arreola *et al.* (2004) for similar parity cows in Australia and Mexico, respectively. Rekik and Ben Gara (2004) also reported that parameter *a* in cows showing the *atypical* curve range from 48 ± 57 to 166 ± 2312 . However, our studies failed to find such big differences in the values of the initial lactation phase of cows with the *atypical* lactation.

Similar findings of higher lactation persistency in first parity compared to higher parity cows as found in this study (Tables 5.2 and 5.4) have been reported (Wood 1969, Grossman *et al.* 1999, Jakobsen *et al.* 2002). Tekerli *et al.* 2000 observed that because of preferential partitioning of nutrients into growth and mammary development, primiparous cows are more inclined to peak later and maintain higher production persistency than more mature cows.

The good fit of the IG model obtained in this study, as indicated by the RMSE (Table 5.2), is comparable to the good fits previously reported, using R^2 values, for fitting the IG model to dairy cow milk yield data (Wilmink 1987, Olori *et al.* 1999, Tozer and Huffaker 1999), although those authors used the log transformed IG model while this study used the non-linear regression approach. The significance of the parameters in this study was determined by the use of confidence intervals, since R^2 is not considered to be useful in non linear regression (Ratkowsky 1990). The presence of serial correlations, as observed in this study, indicating biased predictions at certain lactation stages, are a well documented criticism of the IG model under various production systems (Ali and Schaeffer 1987, Wilmink 1987, Scott *et al.* 1996, Tekerli *et al.* 2000).

5.5.2 Individual cow lactation

Wood's IG model detected three different curve shapes, namely the standard (*typical* or type I), non-standard (*atypical* or type II) and continuously decreasing shapes (Figure 5.2). Differences in curve shapes in dairy cattle (Pérochon *et al.* 1996, Olori *et al.* 1999, Macciotta *et al.* 2005), and in deer (Landete-Castillejos and Gallego 2000) have been

reported. However, the proportion of individual cows showing the *atypical* curve shape (Table 5.3) reported in this study is lower than the values reported for a typical herd (Olori *et al.* 1999, Rekik and Ben Gara 2004) Olori *et al.* (1999) reported that between 20 to 30% of cows showed *atypical* lactation curve types in their study, which was attributed to genetic difference between individuals, but other authors have reported lower values (Macciotta *et al.* 2005).

The occurrence of *atypical* curve shapes have also been considered to be artefacts of the mathematical function (Landete-Castillejos and Gallego 2000, Macciotta *et al.* 2005), unavailable data in early lactation (Cobby and Le Du 1978, Silvestre *et al.* 2006) and environmental factors (Rekik and Ben Gara 2004). The percentage of *atypical* lactations occurring out of 1046, 503 and 55 lactations in the DIM classes 1 to 3 were 17, 6.4 and 5.4, respectively. Therefore, this trend in our study did not support the suggestion that missing test days in early lactation may be responsible for differences in curve shapes (Congleton and Everett 1980).

However, it seems that the trend in the occurrence of *atypical* lactations observed in this study is due either to the peculiar production pattern of pasture-based cows or possibly to an inconsistent sampling or recording pattern at different lactation stages. In a study evaluating the effect of sample size on lactation model performance, Silvestre *et al.* (2006) observed that the performance of the IG and Ali and Schaeffer's PR models were highly affected by the reduction of the sample dimension i.e. number of available test-day records. This phenomenon requires further detailed analysis.

High correlation among the parameter estimates of the IG model (Table 5.5), especially parameters a , b and total milk yield as found in this study, confirmed earlier reports that the parameters of the IG model can be manipulated for improved breeding (Ali and Schaeffer 1987, Rekaya *et al.* 2000). Similar correlations among parameter estimates of the IG model have previously been reported (Tekerli *et al.* 2000). Rekik and Ben Gara (2004) observed that high producing cows (high parameter a) with *typical* curves shapes tended to have the highest peak yield and consequently the highest 305-d yield (Tekerli *et al.* 2000). However,

weak correlations between the EBV index, i.e. Milk EBV, the production APR and ASI indices, and the IG model parameter estimates, seems to suggest that minimal changes in these indices may have little or no effect on the shape of the lactation curve.

The narrow range of goodness of fit in the results, as reflected in the RMSE values (Tables 5.2 and 5.4), as well as marginal difference in the initial lactation and peak milk yield values, suggests that there is little variation in the pattern of lactation of post-2001 individual cows based on EBV choice. It is also possible that the effects of the change in EBV index method is yet to fully filter through considering that the offsprings of cows sired by bulls based on the new indices will only come into lactation in 2004. In addition the production trait components of both EBV measures (ASI and APR), i.e. protein, fat and milk ABV (Australian breeding value) are exactly the same. Therefore, it is possible that the effects of including temperament and survival traits in the APR will reflect more on life time productivity rather than yields per lactation as tested in this study. This assumption is corroborated by the significant differences observed in herd/aggregate data and the lack of such differences attributable to individual cows.

Other factors affecting milk yield apart from genetic factors are parity, lactation stage and persistency, milking practices, cow age, body weight and body condition, metabolic diseases, oestrous cycles, and pregnancy, as well as temporary environment factors such as nutrition (Buckley *et al.* 2003). These other factors affecting curve shapes will be examined in subsequent chapters of this thesis.

5.6 Conclusion

The results of this study indicated that choice of EBV index did not significantly affect the parameter estimates of the IG model, especially in cows selected on the basis of APR. However the higher daily milk yields in HM compared to LM cows confirms that producers should take advantage of the potential of HM cows. Wood's IG function adequately modelled the lactation profile of pasture-based cows, explaining over 90% of the observed herd variation irrespective of whether ASI or APR sire breeding index were used, although individual cow lactations were less accurately predicted. These facts should be borne in

mind when comparing production patterns between herds and individual cows. The absence of stressful peak milk yields and comparable levels of production irrespective of EBV index choice indicate that producers stand to gain by adopting the APR method of choosing breeding sires because of the additional survival and longevity factors included in its computation. It is recommended that the effect of EBV index on the lactation curve pattern should be evaluated after about 5-10 years of implementation.

The poor goodness of fit of individual lactations and the potential influence of other factors apart from sire EBV on lactation curve shapes warrant further exploration of other lactation models. Therefore, the next chapter of this thesis will investigate the goodness of fit of other empirical, mechanistic and test-day models as well as the genetic aspects of the lactation parameters.

Chapter 6. Predictive characteristics of lactation models for pasture-based Holstein-Friesian dairy cows.

6.1 Summary

In Chapter 5, the thesis examined the goodness of fit of the incomplete gamma (IG) model as well as the effect of sire breeding index on the shape of the lactation curve for pasture-based Holstein-Friesian cows. Although the goodness of fit as measured by the root mean square error (RMSE) indicated a good fit to the data, large serial autocorrelations among the residuals were observed. These limitations of the IG model and the lack of the relation of the parameters of the model to the physiological process of lactation, which has been described as being driven by the proliferation and programmed death of cells in the mammary gland, has led to a preference for the use of mechanistic models. Furthermore, the data used in that chapter were based on weekly milk yield records. National and regional data utilised for genetic evaluations in Australia are based on monthly test-day records. Therefore, this chapter has the objective of comparing the predictive characteristics of some of the well-known empirical, mechanistic and semi-parametric models with a view to identifying which of them best describe the lactation data from the pasture-based dairy system using monthly milk yield records and to evaluate the factors affecting the goodness of fit of the models.

Fourteen lactation (8 empirical, 4 mechanistic and 2 semi-parametric) functions were fitted to data for a herd of Holstein-Friesian cows from 241 herds in the state of Tasmania, Australia using the non-linear procedure PROC NLIN in SAS. Four of the functions were further tested by fitting to 8,441 individual cow's milk yield profiles. Model accuracy was evaluated based on RMSE, and the magnitude and distribution of residuals. All the models fitted the typical lactation well but serial correlations among residuals indicate biased predictions at various lactation stages. Lactation curves of individual cows were less accurately modeled. The new three-parameter log quadratic model first introduced here out-performed the incomplete gamma model and had similar goodness of fit as the four-parameter modified gamma model.

6.2 .Introduction

Mathematical functions such as those previously used to describe a series of milk test-day records (Wood 1967, Cobby and Le Du 1978, Wilmink 1987) have the advantage of minimizing random variation while simultaneously summarising the lactation profile into biologically interpretable parameters. The resulting parameter estimates of these models can be further analysed statistically to estimate systematic effects, predict future yields from incomplete lactation records, detect deviation of an individual cow or a herd of cows from the expected performance, and provide early estimates of 305-day milk yields for breeding decisions (Jensen 2001, Schaeffer 2004). The curves can also be incorporated into mathematical models of dairy enterprises to monitor changes in management factors (Morant and Gnanasakthy 1989, Pollott 2000).

The functions available to model lactation profiles are many, and include empirical (linear or non-linear), mechanistic, test-day and non-parametric models (see review by Beever *et al.* 1991 and Chapter 3 of this thesis). The incomplete gamma function (Wood 1967), in spite of its limitations (see Chapters 2), is the most widely used function to model the entire lactation in dairy cows. In order to address some of the limitations of earlier models, other empirical (Yadav *et al.* 1977, Ali and Schaeffer 1987, Wilmink 1987, Eiston *et al.* 1989, Morant and Gnanasackthy 1989, Sherchand *et al.* 1995) models were proposed. However, the need to relate the lactation process to the physiological processes in the mammary gland led to the introduction of the mechanistic model (see Chapter 2) first proposed by Neal and Thornley (1983). Other forms of these models have been developed (Emmans and Fisher 1986, Ferguson and Boston 1993, Dijkstra *et al.* 1997, Grossman and Koops 2003, Pollott 2000 and Pollott 2004). More recently, non-parametric or semi-parametric models, including Legendre polynomials (Kirkpatrick *et al.* 1994), and cubic splines (White *et al.* 1999), have also been proposed as suitable functions to model lactation in dairy animals (see chapter 3). However, despite the better fits obtained from the more complex models, many researchers still prefer to use the simpler empirical models (Tozer and Huffaker 1999).

The shape of the lactation curve is assumed to be the same for all dairy cows, in that it takes the shape of an increase to a peak 4-8 weeks into lactation, followed by a gradual decline until drying up. However, differences in curve shapes due to various

environmental and management factors have been reported by many authors (Olori *et al.* 1999, Val Arreola *et al.* 2004). Lactation curve modelling is of interest because curve shapes can be manipulated in an economically desirable way (Lennox *et al.* 1992, Tozer and Huffaker 1999). Similarly, differences in curve shapes due to genetic and environmental factors (Ali and Schaeffer 1987, Swalve 1999, Tozer and Huffaker 1999, Garcia & Holmes 2001, Schaeffer 2004) suggest that curves shapes are important for meaningful phenotypic and genetic improvement of the dairy cow.

The models tested in this chapter were chosen because the suitability of different models reported in the literature has been diverse and the functions found to be suitable under one production system may be unsuitable in another. For instance, Olori *et al.* (1999) reported that the polynomial model (Ali and Schaeffer 1987) gave the best fit in a farm-based study among the five models considered, while Garcia and Holmes (2001) found no difference in average lactation predicted by both di-phasic and linear-based split-plot models. Papajcsik and Boderó (1988) evaluated twenty lactation models and concluded that the Wood's incomplete gamma (IG) model ($y_t = at^b e^{-ct}$) and its derivative

$$y_t = at^b / \cosh^{(ct)} \quad 6.1$$

gave equally good fits for cows in a sub-tropical environment. Pollott and Gootwine (2000) tested seven models and their derivatives and observed that the modified gamma (MG) model (Morant and Gnanasakthy 1989) and the re-parametrized multiplicative form of the mechanistic model proposed by Pollott (2000) gave the best goodness of fit to weekly milk yield records of dairy sheep. In comparison, Val-Arreola *et al.* (2004) fitted five models to data from small scale and intensive dairy systems in Mexico and found that the mechanistic model presented by Dijkstra *et al.* (1997) gave statistically significant parameter estimates and the lowest error mean squares, while Silvestre *et al.* (2006) evaluated seven mathematical models including three Legendre polynomials and cubic splines and concluded that the goodness of fit of the IG and EXP (Wilmink 1987) models were affected by sampling (data) size. In their study, the cubic splines gave the lowest error mean squares.

The objectives of this chapter were to compare the accuracy of prediction of some of the more commonly used lactation models for pasture-based Holstein-Friesian (HF) cows in

a temperate climate, to identify which models best represent the lactation profile at either a herd or individual cow level and to evaluate the main factors affecting the goodness of fit of these models.

6.3 Materials and methods

6.3.1 Data management

The data used in this study, comprising 271,434 lactation records from 428 dairy herds in six dairy regions collected over the production years 1995–2007, were received from TasHerd, the milk recording organisation in Tasmania. The background to dairying in Tasmania has been discussed in Chapter 2 of this thesis. The data were edited for obvious errors in recording (e.g. calving date preceding birth date). Records where lactation length <100 or >305 days, or where there were less than five test-day records for a particular lactation, were excluded from the analysis. Additional records excluded from the analysis included records of cows with first recorded day in milk from parturition (DIM), $4 > \text{DIM} < 46$ and parity >5 . Only Holstein-Friesian cows were included in the final data set, which consisted of 150,446 records (23,021 lactations from 171 herds). Test-day classes were made such that parities >2 were pooled and referred to as parity 3. Lactation stage in months (Tday) was obtained as number of days from calving divided by thirty except the first test date which comprised days 5–30 post-calving. Summary statistics for herd characteristics as presented in Table 1 shows that most dairy herds are located in the North of Tasmania. The number of herds and cows per herd included in the recording scheme increased from 2005 to 2007 with the exception of the Far North West in 2006. Average daily milk yield did not differ considerably between regions.

The various functions used to evaluate the average daily milk (L/d) of the typical Friesian cow under the production system in Tasmania are shown in Table 6.2. The IG function (Wood 1967) was chosen because it is one of the most widely used functions in lactation modelling (SAS 2004, Silvestre *et al.* 2006). The Morant and Gnanasakthy (1989) function was found to fit cattle data well and according to Pollott (2000) produces uncorrelated parameters. Additional empirical models considered in this chapter were chosen because of the similarity of their parameters to a new log quadratic

polynomial (LQ) function which is described for the first time in this thesis. The mechanistic models of Ferguson and Boston (1993), Dijkstra *et al.* (1997), and Pollott (2000), in addition to fitting lactation data, provide parameters that relate to the biological process of lactation. Two additional semi-parametric functions, being the Legendre polynomial (Kirkpatrick *et al.* 1991) and cubic splines (White *et al.* 1999), were tested because they have been reported to fit lactation data well (Silvestre *et al.* 2006).

6.3.2 The new log quadratic polynomial model

A new second degree polynomial model was proposed as a potential model for modeling lactation in dairy cows. This model has the form of the parabolic equation presented in its standard or vertex form as

$$\text{Log}Y_t = a(b - \text{Log}t)^2 + c \quad 6.2$$

where $\text{Log}y_t$ is the Log_e transformed daily milk yield, $\text{Log}t$ is the log transformed time t in days, weeks or months in milk and $a \neq 0$, b and c are parameters of the model. Parameter a controls the rate of incline to peak or post-peak decline, b is the day at peak yield and c is the peak milk yield, i.e. maximum production when $a > 0$ or minimum production if $a < 0$. Parameters a and b control the axis of symmetry of the curve (the x coordinate of the turning point). Expressed in its general form, the second degree polynomial has the form

$$y_t = ax^2 + bx + c \quad 6.3$$

which can also be expressed as

$$y_t = a \left(x + \frac{b}{2a} \right)^2 - \frac{b^2 - 4ac}{4a} \quad 6.4$$

In this form the turning point of the curve is given by

$$\left(-\frac{b}{2a}, -\frac{\Delta}{4a} \right) \quad 6.5$$

where $\Delta=b^2-4ac$. Equation 6.2 can be expressed in linear form as

$$\text{Log}Y_t=a\text{Log}t^2+b\text{Log}t+c \quad 6.6$$

and solved by ordinary least squares regression. The parameters of the model remain as previously explained.

Table 6.1. Summary statistics for daily milk yields (kg/d) of the data used in the study.

Region	Calving Year	Number of Herds	Number of Cows	Number of Records	Milk yield (L/d)			
					Mean	Min	Max	Stdev
Central North	2005	2	174	1,547	13.1	1.9	43.2	6.09
	2006	15	229	1,757	18.3	2.09	48.3	8.67
	2007	27	4,544	32,643	11.6	2.08	42.3	5.53
Far North West	2005	7	284	1,670	9.4	2.1	30.6	3.95
	2006	13	179	1,347	11.5	2.31	29.8	4.52
	2007	29	3,783	28,743	11.2	2.09	34.7	4.81
King Island	2005	3	7	56	11.0	1.95	21.0	4.89
	2006	9	75	676	11.2	1.95	28.8	4.82
	2007	12	1,078	7,322	10.8	1.17	30.1	5.07
North East	2005	4	38	331	11.1	2.09	25.3	4.17
	2006	17	688	5205	11.1	1.88	28.5	4.59
	2007	35	5,278	43,504	11.3	2.09	34.9	4.74
North west	2005	13	232	1,686	11.8	2.13	31.9	5.60
	2006	20	554	4150	11.1	2.09	35.4	5.11
	2007	27	2,267	18,422	12.1	1.3	59.0	5.38
South	2005	1	30	260	7.7	2.11	15.9	2.64
	2006	2	4	37	11.8	5.4	19.6	3.84
	2007	4	140	1,090	11.1	2.08	28.9	4.25

6.3.3 Statistical analysis

In order to determine the typical lactation curve of pasture-based Friesian cows in Tasmania, all the test-day records were analysed for month in milk (Tday) by PROC GLM, the general linear models procedure of the SAS Institute (SAS 2002), which can handle unbalanced data, using the model

$$Y_{ijklmno}=\mu+H_i+TD_j+CY_k+M_l+P_m+b(Md_{ijklmno}-\overline{Md})^2+e_{ijklmno} \quad 6.7$$

where $Y_{ijklmno}$ is the $ijklmno$ observation on daily milk yields with fixed effects; H_i of i^{th} herd ($i=1, 2 \dots 171$), TD_j of j^{th} test-day ($j=1, 2 \dots 10$), CY_k of k^{th} Calving year ($k=1, 2, 3$), M_l of test month l^{th} ($l=1, 2 \dots 12$), P_m of m^{th} parity ($m=1, 2 \dots 5$), with partial regression coefficients; b of interval between calving and first test-day recording, $(Md_{ijklmno} - \overline{Md})^2$ is the day at first test-day fitted as a covariate, μ is overall mean and $e_{ijklmno}$ is random sampling effect of lactation p with mean zero and variance σ_e^2 . Differences in data sizes between factors included in the model for each region precluded the testing of interaction effects.

The resulting least squares means of test-day milk yields for the ten lactation months provided the average daily milk yields in months (1-10) of lactation subsequently referred to as the typical Tasmanian Friesian cow lactation curve (TFC). These data were fitted to each of the lactation functions in turn using the Marquardt's iterative method of the non-linear (NLIN) procedure of SAS (SAS 2002) to estimate the effect of lactation stage in months (Tday) on TFC. The goodness of fit of each of the models was also tested by substituting Tday in the TFC data with the corresponding mean DIM for each month, i.e. 15 for Tday1, 45 for Tday2 and so on. The models fitted to the TFC were compared based on root mean square error (RMSE obtained as the square root of the error mean square RMS), the magnitude and distribution of residuals and the correlation between observed and predicted milk yield. Other parameters of the model, i.e. peak yield, day at peak, persistency and milk yield to 305d were either calculated using the relevant formula in the original models or derived from the curve. The exponential model of Wilmink has a constant parameter (k) which was fixed (Wilmink 1987) in this study at 0.46, this being the best fitting value for herd mean yield in a preliminary analysis of the data sets, during which the initial values of the NLIN procedures were also determined.

Table 6.2. The functions used to fit the typical Tasmanian Friesian cow lactation

Model	Abbrv	Function	Equation Number	Source	N*
Incomplete gamma	IG _N	$Y_i = at^b e^{-ct}$	6.8	Wood (1967)	3
Incomplete gamma	IG _L	$\text{Log } Y_i = \log(a) + b * \log t - ct$	6.9	Wood (1967)	3
Modified gamma	MG	$\text{Log } Y_i = a - bt' + ct'^2 + d/t$	6.10	Morant and Gnanasakthy (1989)	4
Exponential	EXP	$Y_i = a + be^{-kt} + ct$	6.11	Wilmink (1987)	3
Polynomial	PL	$Y_i = a + b(t/1) + c(t/1)^2 + d(\ln 2) + e(\ln 2)^2$	6.12	Ali and Schaeffer (1987)	5
Bi-compartmental	BC	$Y_i = ae^{-bt} + de^{-ct}$	6.13	Ferguson and Boston (1993)	4
Dijkstra	DJ	$Y_i = a \exp[b(1 - e^{-ct})/c - dt]$	6.14	Dijkstra <i>et al.</i> 1997	4
Pollott	PT	$Y_i = (a/1 + ((1-b)/b) \exp(-cn)) (1/1 + ((1-d)/d) \exp(-en))$	6.15	Pollott (2000)	5
Modified Pollott	MPT ₁	$Y_i = (a/1 + ((1-k)/k) \exp(-cn)) (1/1 + ((1-d)/d) \exp(-en))$	6.16	Pollott (2000)	4
Modified Pollott	MPT ₂	$Y_i = (a/(1 + k \exp(-1(n)))(2 - \exp(et))$	6.17	Pollott (2000)	2
Quadratic polynomial	QP	$Y_i = a + bt + ct^2$	6.18	Dave (1971)	3
Parabolic exponential	PE	$Y_i = a \exp(bt - ct^2)$	6.19	Sikka (1950)	3
Log quadratic polynomial	LQ	$\text{Log } Y_i = a(b - \text{Log } t)^2 + c$	6.20		3
Legendre polynomial	LEG	$Y_i = \sum_{i=0}^n \alpha_i \phi_i(w)$	6.21	Kirkpatrick <i>et al.</i> 1990	5
Cubic splines	SPL	$Y_i = a_i + b_i(t - t_1) + (t - t_1)^2 + d_i(t - t_1)^3$	6.22	Green and Silverman (1994)	4

N* = number of model parameters; Abbrv = Model acronyms

where $y(t)$ is milk yield (L/d), at time t (months and days were considered), a , b , c , d , e , α_i and ϕ are parameters that define the scale and shape of the curve, $t' = (\text{Dim} - 150/100)$, $t_1 = t/305$, $t_2 = 305/t$, $n = (t - 150)$ and k is a constant. In all the MPT models, parameter a is the maximum milk secretion potential, b and d are proportions of milk yield potential and loss at parturition while c and e are the growth and death rate parameters of the two logistic curves respectively. On the other hand, parameters b and c (BC model) and b and d (DJ model) represent the rate of cell proliferation and death, respectively (see chapter 3).

Some background meaning of the parameters of the various functions have been discussed in Chapter 3.

$$\text{In the Legendre polynomial, } w = 2 \left(\frac{t - t_{\min}}{t_{\max} - t_{\min}} \right) - 1 \quad 6.23$$

where $t_{\min} = 1$ and $t_{\max} = 10$.

These functions in Table 6.2 were fitted to the TFC data using PROC NLIN, an iterative non-linear curve fitting procedure in SAS (2002). The parameters of each curve were estimated using the least squares method and the computational strategy of Marquardt was used to search for the 'best fit' solution. The 'best fit' curve was obtained for each lactation when the difference between the error sums of squares in successive iterations was less than 10^{-6} relative to the value of the estimates (Pollott and Gootwine 2000).

Other characteristics of the lactation curve such as the peak yield (PY), day at peak yield (DP), total milk yield to 305 day (CTMY) and persistency of the lactation were calculated for each function. In order to obtain a uniform and comparable value of persistency across functions, persistency was defined in this thesis as the ratio of the difference in daily milk yield at DIM 60 and 270 and the number of days during the same period, expressed in mL/d using the formula

$$P_{\text{lact}} = (MY_{60} - MY_{270}) / 210 \quad 6.24$$

where P_{lact} is the persistency of lactation, MY_{270} and MY_{60} is daily milk yield on DIM 270 and 60 respectively expressed in mL^{-3} . Cows with lower P_{lact} values are more persistent than those with higher values. These days were chosen because for most pasture-based dairy cows peak milk yield would have been attained before or on day 60 post-partum. Similarly, although lactation length could vary in different production systems, under the pasture-based yearly calving system most lactations would last 270 days or beyond. In some cases the calculated values were obtained by inspection and CTMY by summation, after calculating the daily milk yield values for each day of lactation. In other cases they were derived using the various mathematical functions as described in the original papers.

The result obtained from fitting all functions shown in Table 6.2 to the TFC data were used to estimate daily milk yield on the successive 10th day in lactation i.e. DIM = 10, 20, 30 etc, making up 30 predicted values for each of the functions. The residuals of these estimated values were calculated using the TFC values and residual mean squares

(RMS) computed as a measure of goodness of fit using the formula (Pollott and Gootwine 2000):

$$RMS = (\sum_{t=1}^N (M_{rpred} - M_{rtpy})^2) / (N - Q) \quad 6.25$$

where M_{rpred} and M_{rtpy} were the predicted and 'typical' values on each of the chosen days, respectively, N was the number of daily milk records in the lactation (in this case 30) and Q was the number of parameters in the model. The resulting RMS was then ranked in order of best to worst goodness of fit of the functions. This information was used in determining which of the functions should be used in the further analysis of individual cow's lactations. Other factors considered in choosing the subsequent functions are the number of parameters in the function and the correlation among the parameters.

6.3.3 Individual cow lactations

Based on the goodness of fit of all the functions, four models were considered for further investigation. These were the IG, MG, BC and LQ functions. These functions were fitted in turn to 76,762 lactations records (8441 cows), which were all the cows with sire records from four out of the six dairy producing regions of Tasmania and having >5test-day records. The lactations were grouped according to their mean daily milk yield (DY), Minimum day in milk (MID), maximum day in milk (MXD), number of test-days (NTD) and parity (P). These classes are DY: (low $2.83 < DY \leq 11.49$, medium $11.50 \leq DY \leq 16.49$ and high $DY > 16.5$), MID: (early $5 < MID \leq 15$, medium $15 < MID \leq 30$ and late $30 < MID \leq 45$) MXD: (short $119 < MXD \leq 240$, medium $240 < MID \leq 270$ and normal $270 < MID \leq 305$), NTD: (fewer $4 < NTD \leq 7$, few ($7 < MID \leq 9$ and full $9 < MID \leq 11$), and P: (1, 2 and >2). These classes contained (2066, 3221, 3154), (2722, 3887, 1832), (1351, 4245, 2845), (2146, 1963 and 4332) and (2098, 1813, 4530) individual cows respectively.

The four functions were fitted to the 8441 individual lactations using the iterative non-linear curve fitting procedure, as described above. The RMS's obtained from fitting each function to the lactations were then analysed in a combined analysis involving all the functions and also separately for each function. Differences between the goodness of

fit of the 4 functions fitted to the 8441 lactations were investigated using the following model:

$$R_{ij} = LR_i + MOD_j + e_{ij} \quad 6.26$$

where R_{ij} was the RMS derived from fitting the functions to the 76,762 lactation records, LR_i was the i^{th} lactation record ($i=1\ldots 8441$), MOD_j was the j^{th} model function ($j=1\ldots 4$) as shown in Table 6.6 and e_{ij} was the error term. Differences between the means were tested using the least significant difference (lsd) method. To detect the effect of DY, MID, MXD and NTD classes on the goodness of fit, a least squares procedure was used fitting a general linear model, with the following model:

$$R_{ijklm} = DY_i + MID_j + MXD_k + NTD_l + P_m + e_{ijklm} \quad 6.27$$

where R_{ijklm} was the RMS derived from fitting a particular function to the 8441 lactation records, DY_i was the i^{th} mean daily milk yield ($i = 1\ldots 3$), MID_j is the j^{th} minimum recorded day in milk, ($j=1\ldots 3$), MXD_k is the k^{th} maximum recorded day in milk ($k=1\ldots 3$), NTD_l is the l^{th} number of test-day records ($l=1\ldots 3$), P_m is the m^{th} parity ($m=1\ldots 3$) and e_{ijklm} was a randomly distributed error term. The interaction terms were inestimable due to differences in the size of the various classes and were dropped from the final model. Least squares means, within an effect, were compared and the paired differences between levels within an effect were tested using the least significant difference method.

6.4 Results

6.4.1 Typical lactation

Figure 6.1 shows the profile of the TFC based on the least squares means of monthly Tday derived from fitting the entire 150,446 records to equation 6.7. Milk yield (L) started at 12.6 during the first month in lactation, attained peak level about 50d post-partum at 13.2 and then declined gradually before reaching nadir at 8.9 at the end of lactation. Milk yield declined throughout lactation except from the first to the second month in milk when it increased by an average of 0.40L (Figure 6.1). Root mean square error (RMSE) of predicted TFC milk yield was generally higher in the mechanistic

compared with the empirical models, the DJ being the exception (Table 6.3). It should be noted that the results of fitting the TFC to the mechanistic functions could not be entirely reliable due to error messages. Among the three parameter empirical models, RMSE was highest in the QP and PE functions, followed by the IG models and lowest in the LQ. The PL (5 parameter) and MG(4 parameter) fitted the typical lactation curve data better than the three parameter models with the exception of the LQ and MG model which had the lowest RMSE of all the models tested.

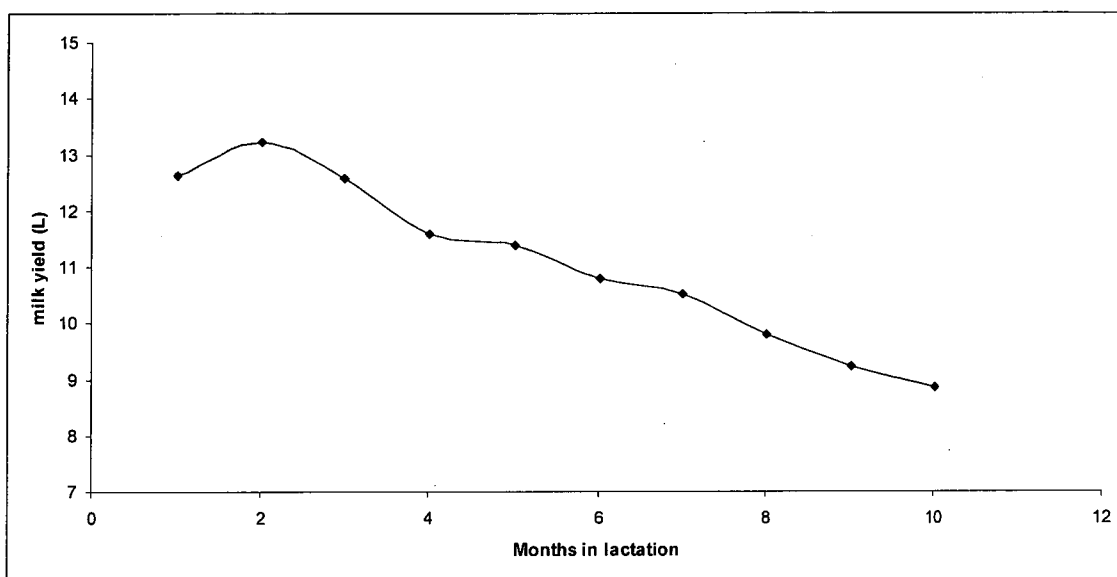


Figure 6.1. The average lactation curve obtained from the analysis of daily milk yield data of 23,021 Friesian cows.

Table 6.3. Lactation parameter estimates and the root mean square error (RMSE) of the functions fitted to the typical Friesian cow lactation data based on monthly test-days.

Model	Typical Friesian lactation Function	N	RMSE
IG _N	$Y_t = 13.718 t^{0.0934} e^{-0.0661t}$	3	0.2488
IG _L	$\text{Log } Y_t = \log(13.704) + 0.089 \cdot \log t - 0.065t$	3	0.0205
MG	$\text{Log } Y_t = 2.684 - 0.066t' + 0.001t'^2 - 0.175/t$	4	0.0589
EXP	$Y_t = 14.489 - 1.5387e^{-0.46t} + 0.574t$	3	0.2888
PL	$y_t = -225.14 + 1803.012t_1 - 15266.39t_1^2 + 78.77 \ln t_2 - 6.679(\ln t_2)^2$	5	0.1597
BC*	$Y_t = 11.559e^{-0.043t} + 0.043e^{-2.370t}$	4	0.3519
DJ*	$Y_t = 0.060 \exp(22.631(1 - e^{-4.126t})/4.126 - 0.049t)$	4	0.1766
PT**	$Y_t = (1E^{-8}/1 + ((1 - 0.999)/0.999) \exp(-0.043n)) * (1/1 + ((1 - 0.048)/0.048) \exp(-0.0004n))$	5	0.4062
MPT ₁ **	$Y_t = (4.831/1 + ((1 - 0.999)/0.999) \exp(-0.124n)) * (1/1 + ((1 - 1.102)/0.048) \exp(-0.015n))$	4	0.2307
MPT ₂ **	$Y_t = (13.57/(1 + 0.00010001) \exp(-1(t - 150))) \times (2 - \exp(0.793t))$	2	0.2307
QP	$Y_t = 13.437 - 0.338t + 0.013t^2$	3	0.314
PE	$Y_t = 13.333 \exp(-0.019t - 0.002t^2)$	3	0.306
LQ	$\text{Log } Y_t = -0.121(0.518 - \text{Log } t)^2 + 2.573$	3	0.017
LEG	$Y_t = \sum_{i=0}^n \alpha_i \phi_i(w)$ the terms in the model are Tday=1.558 and 3 Leg(Tday,3) terms being 3.567, -7.552, and 0.1274	4	0.304
CS	$y_t = a_i + b_i(t - t_i) + c_i(t - t_i)^2 + d_i(t - t_i)^3$ The three terms in the model are Tday=-0.4828, mu=13.73, and spl(Tday3)=-0.022	3	0.307

Models are as previously defined in table 6.2.

* Either model did not converge or converged with errors message

† a is the milk secretion potential, b and d are the proportions of secretion potential and loss achieved at parturition and c and e are the growth and death rate parameters of the two logistic curves. Parameter b was replaced by 0.9999 and n = (t - 150) in all Pollott models (Pollott, 2000).

Correlation between predicted and observed milk yields was highest in the PL model at 0.997 and lowest in the PT model (0.764). Correlations of predicted and observed yield were generally similar in all the models being and average of 0.989. The plots of some of the best fitting lactation functions are shown in Figure 6.2. The MPT₂ and the QP models fitted a continuously declining lactation curve in contrast to a curve rising to a peak before the decline. Although depicted in the curve, the incline to peak yield was not as conspicuous in the IG and MG functions. The PL and LQ models gave the best fitting curves to the TFC data.

The residuals derived from fitting the various functions to the typical lactation data are shown in Figure 6.3. The non-linear form of the IG and the EXP model under-predicted milk yield, in early lactation, and over-predicted peak milk yield. The PL model over-

predicted yield during mid-lactation and under-predicted towards the end of lactation. The lowest residuals were obtained from fitting the MG and LQ model. Of the mechanistic models, the BC, PT and MPT₂ functions had similar levels of inaccurate predictions as the IG model while the DJ models under-predicted milk yield during mid-lactation. Both of the semi-parametric models under-predicted milk yield in early lactation and over-predicted peak and mid-lactation milk yields.

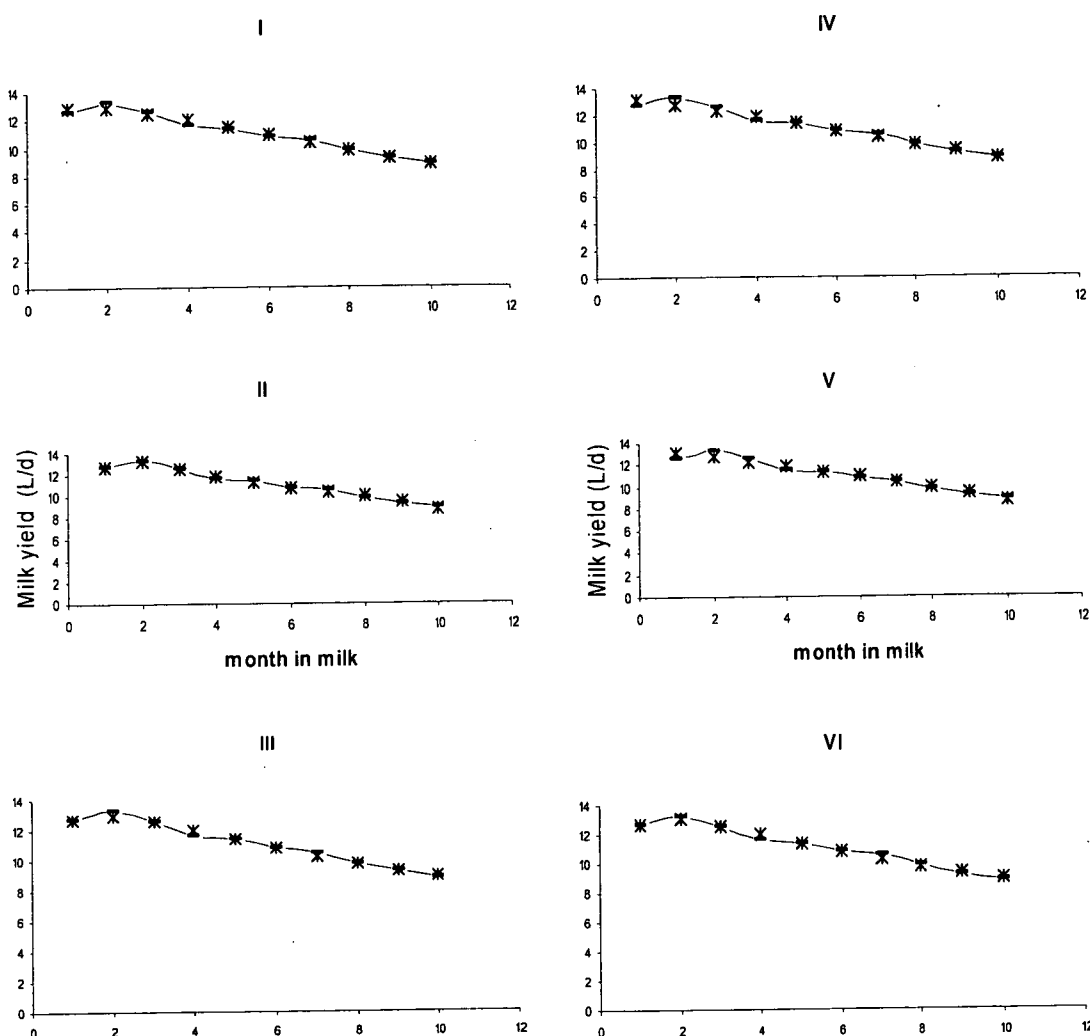


Figure 6.2. Representative lactation curves derived from fitting the typical Friesian cow lactation data to various models based on monthly test-days.

Models are I-VI * = the predicted daily milk yields of the

$$IG=Y_i=13.718t^{0.0934}\exp^{-0.0661t};$$

$$PL=Y_i=-225.14+1803.012t_1-15266.39t_1^2+78.77\ln t_2-6.679(\ln t_2)^2,$$

$$MG=\text{Log}Y_i=2.684-0.066t+0.001t^2-0.175/t$$

$$MPT_2=Y_i=(13.57/(1+0.00010001)\exp(-1(t-150))) (2-\exp(0.793t)),$$

$$QP=Y_i=13.437-0.338t+0.013t^2 \text{ and}$$

$$LQ=\text{Log}Y_i=-0.121(0.518-\text{Log}t)^2+2.573.$$

— =the actual values of the respective functions

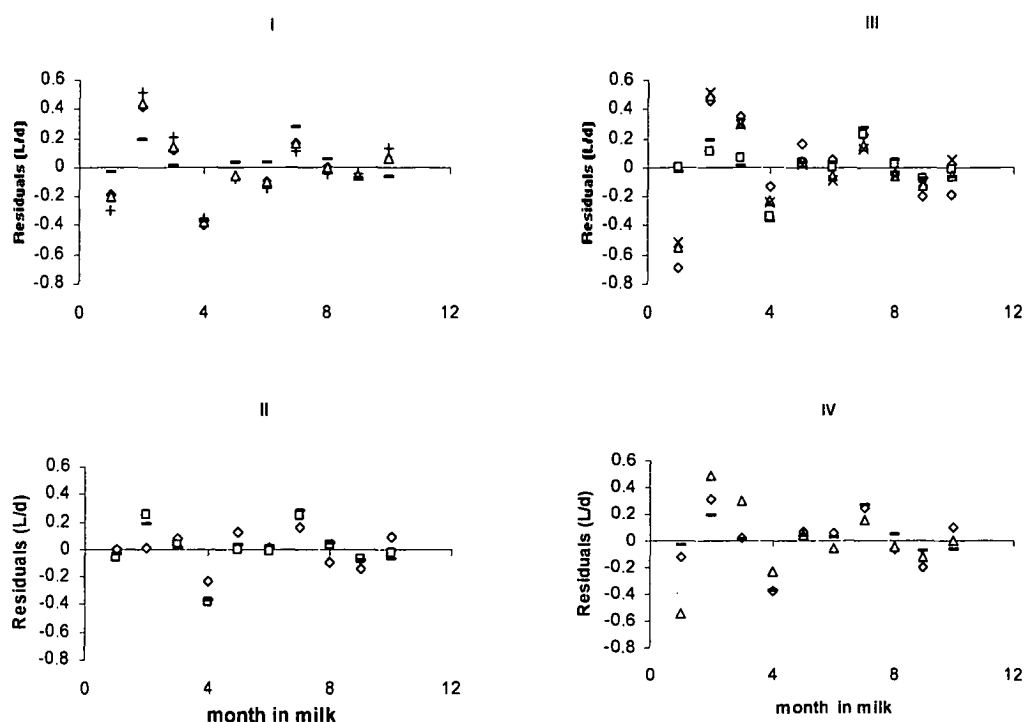


Figure 6.3. The residuals derived from fitting the typical Friesian cow lactation data to various models. Models are

- I Three parameter empirical models; \diamond Wood (IG) Non linear, Δ Wood (IG) log linear, + Wilmlink (EXP), and — Log quadratic
- II Four and five parameter empirical models compared with LQ; Models (number of parameters in parenthesis) are \diamond = Ali and Schaeffer's polynomial PL (5), \square = Morant MG(4), and — Log Quadratic LQ(3)
- III Mechanistic models compared with LQ; Models (number of parameters in parenthesis) are \diamond Bi-compartmental BC(4), \square = Dijkstra DJ(4), Δ Pollott PT(5) \times Modified Pollott, PT₂ (2) and — Log Quadratic LQ(3)
- IV Semi-parametric models compared with LQ; Models (number of parameters in parenthesis) are; \diamond Legendre polynomial LEG (4), Δ Cubic Spline SPL (2)

6.4.2 Lactation functions fitted to the typical Friesian lactation data with DIM time component

Fitting the TFC data with the time component in days in milk (DIM) rather than monthly test-days to all the lactation functions generally improved the goodness of fit in all the empirical models (Table 6.4) as shown by the lower RMSE values with the exception of the LQ model which had the same RMSE irrespective of the time component. On the other hand, the goodness of fit of the mechanistic models were poorer (higher RMSE values), the exception being the PT model. The goodness of fit of the semi-parametric models remained similar irrespective of the form of the time

component of the data. Lactation parameter estimates and the RMSE's of all the models are shown in Table 6.4.

Table 6.4. The mathematical functions, the parameter estimates, and the root mean square error (RMSE) used to fit the typical Tasmanian Friesian cow lactation data based on day in milk (DIM).

Model	Typical Friesian lactation Function	RMSE
IG _N	$Y_t = 11.13t^{0.0626}e^{-0.0021t}$	0.2304
IG _L	$\text{Log}Y_t = \log(11.21) + 0.060 \cdot \log t - 0.002t$	0.0191
MG	$\text{Log}Y_t = 2.696 - 0.0019t + 0.00000269t^2 - 1.945/t$	0.0173
EXP	$Y_t = 13.825 - 904.2e^{-0.46t} + 0.018t$	0.1847
PL	$y_t = -10.22 + 28.84t_1 - 10.29t_1^2 + 15.44 \ln t_2 - 2.76(\ln t_2)^2$	0.1596
BC*	$Y_t = 8.38e^{-0.0014t} + 5.25e^{-0.0014t}$	0.3518
DJ*	$Y_t = 0.024 \exp(12406(1 - e^{-3120.9t})/3120.9 - 0.00000001t)$	10.45
PT**	$Y_t = (1E^{-8}/1 + ((1 - 0.083)/0.083)\exp(0.001n))$ $(1/1 + ((1 - 2.39e^{-62})/2.39e^{-62})\exp(2.24e^{-62}n))$	0.3518
MPT ₁ **	$Y_t = (3.760/1 + ((1 - 0.999)/0.999)\exp(+0.121n))$ $(1/1 + ((1 - 0.071)/0.071)\exp(-0.018n))$	8.932
MPT ₂ **	$Y_t = (-0.697/(1 + 0.00010001)\exp(-1(t - 150))) (2 - \exp(0.011t))$	10.378
QP	$Y_t = 13.264 - 0.012t - 0.00001t^2$	0.314
PE	$Y_t = 4.33e^{-90} \exp(-0.130t - 0.100t^2)$	0.306
LQ	$\text{Log}Y_t = -0.086(3.501 - \text{Log}t)^2 + 2.590$	0.017
LEG	$Y_t = \sum_{i=0}^n \alpha_i \phi_i(w)$ the terms in the model are Tday=0.0548 and 3 Leg(Tday,3) terms being 4.059, 7.811, and 0.112	0.314
SPL	$y_t = a_i + b_i(t - t_i) + c_i(t - t_i)^2 + d_i(t - t_i)^3$ The three terms In the model are Tday=-0.016, mu=13.45, and spl(Tday3) = -0.022	0.307

where $y(t)$ is milk yield (Litres/day), at time t (days), a, b, c, d, e, α_i and ϕ are parameters that define the scale and shape of the curve, $t' = (\text{Dim} - 150/100)$, $t_1 = t/305$, $t_2 = 305/t$, $n = (t - 150)$ and $k = 0.46$ is a constant. Models are

IG = Incomplete gamma, IG_L=Linear form of IG Wood (1967),
MG=Modified gamma (Morant and gnanasakthy 1989), EXP=Exponential (Wilmink 1987),
PL= polynomial (Ali and Schaeffer 1987), BC=Bicompartmental (Ferguson and Boston 1993),
DJ= Dijkstra (Dijkstra *et al.* 1997), PT=Pollott, (Pollott 2000), MPT₁=Four parameter modified pollott, MPT₂=Two parameter modified Pollott,
QP=Quadratic polynomial (Dave 1971), PE=Parabolic exponential (Sikka 1950),
LQ=Log Quadratic, LEG=Legendre polynomial (Kirkpatrick *et al.* 1990) and
SPL=Cubic splines (Green and Silverman (1994)

Fitting the typical Friesian lactation data with the time component in days (DIM) also tended to increase the correlation among parameter estimates of the IG model more than

that observed in the other models (not shown on tables). For instance, the correlation between parameters a and b (IG_N) increased from -0.037 (fitting Tday) to -0.98 (fitting DIM) and from -0.47 to -0.98 (IG_L) respectively, whereas the margin of difference in the correlation of the same parameters in the MG model was only 0.01 units. In comparison, the correlation between parameters a and b declined only marginally being 0.04 (EXP), 0.02(PL) and 0.05(LQ) when the TFC data with DIM was fitted to the functions. The difference in the correlation between parameters a and c was even greater being an increase of 0.75 and 0.64 units for the non-linear and log transformed IG models respectively compared with an increase of 0.01(MG), 0.06 (EXP) and 0.20 (LQ). The correlation between parameters b and c either declined marginally or remained unchanged irrespective of the form of the TFC fitted. Fitting the TFC data with the DIM as the time component affected the performance of the mechanistic models with most of them not attaining convergence or returning parameter values outside the range of expected values.

6.4.3 Milk yield parameters

The predicted milk yield parameters of all the functions are shown in Table 6.5. The MG and LQ models gave initial milk yield values closest to the actual typical lactation data. All the other models over-predicted (IG, IG_L , BC, PT, QP, LEG and SPL) or under-predicted (EXP and PL) initial milk yield. All the models over-predicted peak milk yield by between 0.6 to 1.4L. The EXP and LEG models most accurately predicted the day on which peak yield occurred. The IG and the LQ models over-predicted day at peak by up to 10 days while the mechanistic and SPL models under-predicted day at peak by as much as 17 days. The LQ model gave the most accurate CTMY being only one litre different from the TFC data. All the models except the EXP and PL over-predicted CTMY. The IG model over-predicted CTMY by 41L while the MG model over-predicted by 232L. All the models predicted lactation persistency within 1.5 to 9.6 mL per day but the LQ and EXP models gave the most accurate prediction.

6.4.4 Models selected for further analysis

All the tested functions were ranked in order of best to worst goodness of fit based on the comparison of RMS values calculated from equation 6.25. The order was PL, LQ, IG_L , IG_N , SPL, QP, BC, LEG, PT, MG, EXP, MPT_1 DJ, MPT_2 and PE. Additional

factors that were considered in selecting the final four models are the number of parameters in the model and the magnitude and distribution of the residuals (Table 6.2 and Figure 6.3). Based on these factors, three empirical models LQ, MG and IG_N were selected, the PL model having been dropped as it is a five parameter model. A mechanistic model was selected for because apart from fitting the lactation data, it offers insight into the biology of the lactation process. The BC model, being the best performing among the mechanistic models, was selected. The SPL model had lower RMS than the BC model but its parameters are difficult to relate to either the physical component or the physiological process of lactation.

6.4.5 Individual cow's lactations.

The least squares analyses of the RMS from fitting the four selected models to the 8441 individual cow's lactation are shown in Table 6.6. The BC model fitted individual cow's lactation least accurately followed by the IG model. There is no significant difference ($P=0.63$) in the goodness of fit of the MG and the LQ models. The effects of DY, MID, MXD, NTD and parity on the goodness of fit of the four models (RMS) also shown in Table 6.6 indicated that except for parity (IG and MG) all the factors significantly ($P<0.05$) influenced the RMS values of the various functions. Whereas the IG and BC functions fitted the data from high producing individual cows least accurately, the MG and LQ models fitted the data better than those of medium and low producing cows. Minimum day at first test-day record affected the goodness of fit of all the models with the IG and BC models being the most profoundly affected. The completeness of lactation beyond 270 days and the number of available records >8 did not improve the goodness of fit in any of the models.

Table 6.5. Predicted initial, peak, day at peak, total yields and persistency of lactation obtained by fitting various models to the typical Friesian cow lactation data.

Model	Predicted milk yield parameters ⁺						
	Initial	Peak	Peak day	Nadir	Nadir day	305d Yield	Persistency (mL/d)
Actual	9.73	14.2	21	7.98	264	3313	19.6
IG	12.0	12.9	31	8.65	305	3354	16.8
IG ₁	12.1	12.9	30	8.57	305	3334	16.9
MG	9.07	13.2	34	9.07	4	3545	10.7
EXP	-130	13.4	22	-130	4	2945	18.0
PL	5.20	13.5	30	5.23	4	3303	10.0
BC	13.9	13.6	4	8.89	305	3341	15.2
DJ [*]	-	-	-	-	-	-	-
PT	12.8	12.8	4	9.46	305	3335	10.9
MPT ₁ [*]	-	-	-	-	-	-	-
MPT ₂ [*]	-	-	-	-	-	-	-
QP	13.2	13.2	4	8.67	305	3351	15.3
PE [*]	-	-	-	-	-	-	-
LQ	9.05	13.3	33	8.67	305	3312	18.1
LEG	12.5	13.1	21	9.07	277	3326	16.5
SPL	13.4	13.4	4	8.54	305	3321	16.2

^{*}Although convergence criteria were met, parameter estimates were outside normal range of expected values.

⁺Except for days at peak and nadir, all milk yield parameters are in litres.

Table 6.6. Table 6.6 Least squares means of the effect of average daily milk yield (DY), minimum (MID) and maximum (MXD) days in milk and number of test-day records (NTD) classes on the residual mean square (RMS) derived from fitting four lactation functions to individual cow lactations.

Factors *	Levels	Lactation functions *			
		IG	LQ	MG	BC
Model RMS‡		9.38 ^b	0.20 ^c	0.20 ^c	9.70 ^a
DY	Low	8.45 ^b	0.061 ^a	0.058 ^a	5.04 ^c
	Medium	8.75 ^b	0.045 ^b	0.044 ^b	9.57 ^b
	High	10.59 ^a	0.031 ^c	0.029 ^c	14.35 ^a
SED		0.378	0.0009	0.0006	0.168
MID	Early	8.17 ^c	0.047 ^a	0.044 ^{ab}	11.06 ^a
	Medium	10.38 ^a	0.048 ^a	0.046 ^a	8.71 ^c
	Late	9.24 ^b	0.043 ^b	0.042 ^{ab}	9.19 ^b
SED		0.368	0.0009	0.0006	0.163
MXD	Short	7.81 ^b	0.045 ^b	0.045 ^a	8.81 ^c
	Medium	8.59 ^b	0.042 ^b	0.040 ^b	9.66 ^b
	Normal	11.39 ^a	0.051 ^a	0.047 ^a	10.49 ^a
SED		0.439	0.001	0.0001	0.194
NTD	Fewer	8.14 ^b	0.032 ^c	0.028 ^c	7.26 ^a
	Few	9.89 ^a	0.051 ^b	0.047 ^b	9.99 ^b
	Full	9.76 ^a	0.055 ^a	0.058 ^a	11.72 ^a
SED		0.424	0.0009	0.0001	0.188
Parity	1	8.97	0.045 ^b	0.043	9.01 ^c
	2	9.06	0.045 ^b	0.044	9.57 ^b
	3	9.77	0.048 ^a	0.045	10.38 ^a
SED		0.375	0.0009	0.0009	0.166

Values in the mean RMS column with the same superscript are not significantly different.

‡a,b,c Model RMS of entire 8441 Individual lactations. Group least squares means in the same row with the same superscript are not significantly different.

‡ Standard error of difference (SED) of the four models is 0.019

*Lactation functions are

IG=Incomplete gamma (Wood 1967) as $Y_{(t)} = a t^b e^{-ct}$

LQ=Log quadratic (New model) as $\text{Log } Y_{(t)} = a(b - \text{Log } t)^2 + c$

MG = Modified gamma (Morant and Gnanasakthy (1989) as $\text{Log } Y_{(t)} = a - bt' + ct'^2 + d/t$

BC = Bi-compartmental model (Ferguson and Boston 1993) as $Y_{(t)} = a e^{-bt} + d e^{-ct}$

Models have 3, 3, 4 and 4 parameters respectively.

Number of observations are DY= 3239, 3236, 3807, MID = 2722, 3887, 1832, MXD = 1351, 4245, 2845, NTD = 2146, 1963 and 4332 and P = 2098, 1813, 4530 for the three levels respectively.

6.5 Discussion

In this chapter, the fitting of lactation curves to data from pasture-based dairy systems was taken further by evaluating the goodness of fit of fourteen lactation functions including a new function (presented here for the first time). Comparison of their predictive characteristics permits the identification of a suitable mathematical model to describe and provide a better perspective on the shape of the lactation curve under the Tasmanian production system. Although most of these functions have been previously fitted to lactation data from different production systems, evidence from the literature suggests that different functions are more suited to data from certain production systems (Papajcsik and Boderó 1988, Olori *et al.* 1999, Val-Arreola *et al.* 2004), animal species (Portolano *et al.* 1996, Landete-Castillejos and Gallego 2000, Pollott and Gootwine 2000, Macciotta *et al.* 2005), and physiological condition (Olori *et al.* 1999, Tozer and Huffaker 1999). The mathematical form of the model has also been reported to influence the goodness of fit to lactation data (Landete-Castillejos and Gallego 2000, Silvestre *et al.* 2006).

6.5.1 The typical Friesian cow lactations

Eight empirical functions, namely the two forms (non-linear and log-linear) of the IG, the MG, PL, EXP, QP, PE and the new LQ model were evaluated for goodness of fit to the TLC. All these models had three parameters, except for MG and PL, which had 4 and 5 parameters, respectively. Most of the empirical models under-predicted initial milk yield and over-predicted peak milk yield. These are consistent with the results of under-prediction of daily milk yield in early lactation and over-prediction of peak yields often reported with respect to both forms of the IG model (Olori *et al.* 1999, Pollott and Gootwine 2000) and the EXP and PL models (Silvestre *et al.* 2006). Fitting the two forms of the IG models to the TLC data showed some marked differences in the values of the parameter estimates and the RMS although the log linear form of the model reduced the error of prediction as previously noted by Cobby and Le Du (1978), Congleton and Everett (1980) and Morant and Gnanasakthy (1989). The MG, PL and the LQ model most accurately predicted the TLC (Tables 6.4 and 6.5 and Figures 6.2 and 6.3).

The original gamma function of Wood (1967), used in its \log_e form and fitted using the non-linear iterative approach tended to underestimate the yields in early lactation, overestimate peak yield and underestimate yield during mid-lactation (Figure 6.2). Although the log linear form fitted the data with less error compared with the untransformed version of the model the residuals are not random about the values of day in milk (Figure 6.3). The better fit of the log-transformed version of the IG model reported here is in agreement with the findings of Cobby and Le Du (1978) and Pollott and Gootwine (2000), who reported that the \log_e transformed IG model fitted using the non-linear procedure always yielded more randomly distributed residuals than the version fitted as a linear model. It was already observed in the study of Cobby and Le Du (1978) that the need for log transformation of data was occasioned by the then limitation in computer processing speed. Computer speed in the processing of non-linear models is no longer an issue with the current advancement in computer technology.

The distribution of the residuals of the other empirical, mechanistic and semi-parametric models except the PL, MG, LQ, DJ and LEG models were not random with respect to day of lactation (Figure 6.3). The PL, MG, LQ, DJ and LEG models also had the lowest RMS values, suggesting better fits to the data. However the PL, MG, DJ and LEG models have at least one parameter more than the LQ model. The improved goodness of fit observed with the PL and MG is due to the flexibility of these models in representing environmental perturbations that may account for changes in the production pattern during mid to late lactation. The distribution of the residuals of the MG model (Figure 6.3) showed that this model did not achieve accurate prediction of milk yields in early lactation up to the day at peak yield. According to Pollott and Gootwine (2000), any model that will improve on the IG model should be capable of representing early and peak milk yields more accurately than does the IG model. The LQ model achieves this to a reasonable degree with three parameters that are easier to interpret.

The IG model overestimated initial milk (L) yield by 2.4 compared with an underestimation by the MG and the LQ models of 0.65 to 0.67, respectively. Similarly, CTMY was overestimated by all the models by an average of 50.4L (Table 6.5), except for the EXP and the PL models, which slightly under-predicted CTMY. These results confirmed earlier findings on the prediction characteristics of the IG and PL (Olori *et al.*

1999, Sylvestre *et al.* 2006), IG and MG (Morant and Gnanaskthy 1989, Pollott and Gootwine 2000), and LEG and SPL (Sylvestre *et al.* 2006) models. The sensitivity of models to different data has been reported (Tozer and Huffaker 1999, Val-Arreola *et al.* 2004) and the flexibility of the PL (Olori *et al.* 1999), LEG and SPL models (Sylvestre *et al.* 2006) and variation due to individual cow's milk yield pattern (Olori *et al.* 1999) is also confirmed by results in this study.

There were high correlations among the parameters of most of the models (not shown on the tables). The very low correlations (-0.20 to -0.47) between parameters a vs. b and c (IG) model obtained from fitting the equation 6.2 and 6.3 to the data based on ten monthly yields i.e. ($t=1 \dots 10$) were not repeated when the same model was fitted to the data based on DIM (t ranged from 15-285). Most of the other models maintained similar levels of correlations among their parameter estimates irrespective of the time component of the model. Only the LQ model maintained low correlations between parameters a vs. c and b vs. c , the time component of the model notwithstanding. This pattern of correlations among parameter estimates of the IG model would suggest that care must be taken when comparing the characteristics of the model using different time components. According to Draper and Smith (1966), high correlations among the parameter estimates is indicative of a poorly conditioned sum of squares surface and results in slow convergence of any iterative estimation procedure. In addition, Ratkowsky (1990) had argued that the correlation among parameter estimates of a model does not imply good or bad fitness to data and therefore should not be a basis for judging the goodness of fit a model.

Desirable as the mechanistic models are because of their potential to reveal aspects of the biology of lactation, their performance was not as satisfactory with these data sets due to non-convergence and inestimable parameter estimates. Similarly, the RMS values obtained from these models were higher (indicating poorer goodness of fit) than those from the simpler empirical models. This contrasts with the results reported by Pollott (2000) and Val-Arreola *et al.* (2004). The latter had reported that the DJ model achieved better goodness of fit and lower RMS values compared with four other models including the IG and PT models. The same study, however, also reported that none of the parameter estimates of the PT model was significant indicating less goodness (same as observed in this study) in fitting their data compared with the DJ model. The poor fit

of the PT model was attributed to the representation of cell differentiation and decline in cell numbers by two logistic curves, which increases the parameters to be estimated to 6. This contributes to an over-parameterized model. Results obtained here also failed to substantiate the findings reported by Val-Arreola *et al.* (2004) concerning the DJ model.

On the practicality of using the PT model, Pollott (2000) had observed that the current practice of monthly recording of milk yields, with at most 10 records per lactation may lead to overparametrization if the full PT model was fitted to such data. Our results also showed that the modified PT model with four parameters fitted the data better than the full multiplicative (5 parameter) model although the two parameter form performed worse than both. Options to reduce the number of parameters used in the models include setting $a=d$; estimating the curves at, say, $t \geq 200$ and setting $b=0.99999$, dropping the term for secretion rate from the model entirely and setting c to zero. Additional suggestions for improving the goodness of fit of the curve are the use of standard values in place of certain parameter values, especially the use of a standard value for c . However, some of these options attempted in the modified version of the PT model (Tables 6.2 and 6.3) still did not improve the model performance.

6.5.2 Individual lactations

Although the general shape of the lactation curve is an incline to peak followed by a decline (*typical* lactation), other shapes such as a continuously declining curve or a decline followed by an incline (*atypical* types) are not uncommon (Olori *et al.* 1999, Macciotta *et al.* 2005). The occurrence of individual cows with the atypical production pattern reported to be about 30% in a typical herd (Olori *et al.* 1999) have been reported in dairy cows (Macciotta *et al.* 2005), sheep (Cappio-Borlino *et al.* 1997) and deer (Landete-Castillejos and Gallego 2000). The mathematical principles behind the description of the entire lactation are therefore understandably patterned at fitting first an incline and then a decline part (Cobby and Le Du 1978, Papajcsik and Boderó 1988, Morant and Gnanaskthy 1989). Even the mechanistic models of lactation that have been developed based on the known biological process of lactation (Ferguson and Boston 1993, Dijkstra *et al.* 1997, Pollott 2005) to provide parameters that have biological interpretation are based on the status and dynamics of mammary parenchyma cells during pregnancy and lactation, as these affect the milk production process. According

to Knight and Wilde (1993) and Knight *et al.* (1998) three major processes underlying the lactation process are the mammary parenchyma cell proliferation, their differentiation into active secretory cells and the reduction in their numbers due to programmed cell death (apoptosis). Therefore, most of the existing lactation models are capable of detecting these different curves shapes at the expense of computational compromise (Macciotta *et al.* 2005, Silvestre *et al.* 2006). A desirable model should be simple, capable of mimicking the biological process, and flexible enough to account for the influence of environmental factors affecting the curve shape without compromising too much on accuracy.

All the models yielded higher mean RMS values for individual cows (compared to the TFC data), especially where a large deviation in yield or missing data resulted in poor fits. The effect of the influence of mean daily milk yield (DY), insufficient milk records in early lactation (MID), lactation length (MXD) and the number of test-day records (NTD) on the goodness of fit of individual cow's lactation was investigated and the results (Table 6.6) confirmed earlier findings on the significant influence of these factors on the goodness of fit (RMS) of the four selected models. Silvestre *et al.* (2006) had reported that the goodness of fit of the IG, EXP and the PL models are highly affected by sample properties (size and dimension), especially when the interval between calving and the first test-day increased or when the interval between test-days are lengthened. Similar results were reported by Berry *et al.* (2005), who evaluated different recording schemes using the general linear models. According to Pollott and Gootwine (2000), reducing the number of parameters in a model tended to reduce the accuracy of the model. The poor goodness of fit of many models to individual cow's lactation is due to the poor fitting of the incline to peak yield part of the model, since this is the section often with one (or no) data point, whereas the decline portion was the phase with the most data points.

However, the findings in this study differ from the results of Silvestre *et al.* (2006) in that although the goodness of fit was poorer when the first test-day post-calving increased from 4-15 to 15-30 days, it improved when the interval from calving to first test-day increased to 31-45 days. The restriction of our data sets to only records with minimum first test-date up to 45d, minimum number of lactation records to five and the relatively fewer number of observations in the 31-45 days class (1832) compared with

2722 (4-15d class) and 3887 (15-30d class) might be responsible for the improved goodness of fit observed in cows whose first test date records occurred late in lactation.

The poorer goodness of fits of individual cow's lactation compared to a herd or homogenous groups of cow's lactation is an indication of the biological variability inherent in all biological organisms, the influence of environmental factors (Wood 1969, Olori *et al.* 1999) and possibly due to sample size. Milk production in pasture-based dairy cows is especially prone to fluctuations due to the influence of climatic factors on the nutritive quality, especially the metabolisable energy content, of pastures (Kolver and Muller 1998). In Australia, dairy cows rely on fodder from pasture for 60-70% of the feed energy source (Dairy Australia, 2008). The data used this study came from the whole of Tasmania, where six dairy regions have been identified based on slight variations in micro-climate and the resulting differences in the calving season patterns across regions. In addition, the incidence of high peak and sharp post peak milk yield decline have been reported to be associated with metabolic stress and disease conditions (Collard *et al.* 2000, Tekerli *et al.* 2000), which in turn, can affect the goodness of fit of a lactation model.

Lactation curve shapes have been shown to be affected by parity, mainly due to a less well-defined peak (related to high variability at the beginning of lactation) and greater persistency in first-parity cows (Sherchand *et al.* 1995; Scott *et al.* 1996, Tekerli *et al.* 2000). Differences in the goodness of fit (RMS) due to parity were significant in the LQ and DJ models but not in the IG and the MG models. These differences are related more to the presence or absence of peak of production than to a more gradual decline in second and higher lactations.

A desirable model of lactation should be simple, capable of mimicking the biological process and flexible enough to account for the influence of environmental factors affecting the curve shape without compromising too much on accuracy. In addition, it should be able to fit data from short lactations or standard test-day records (Pollott and Gootwine 2000). These attributes are found in the MG and LQ models. The better performance obtained from fitting the LQ model might be a result of both the transformation of daily milk yield and the weighting applied to time. Pollott and Gootwine (2000) had observed that the fitting of the weighted Wood IG linear function

suggested by Cobby and Le Du (1978) improved the goodness of fit of the typical “Awassi” sheep during early lactation. These attributes of the LQ model and the better fitting throughout lactation with fewer parameters than the PL and MG models suggest that it is a better fitting model than the IG model.

6.6 Conclusion:

Fourteen models were evaluated for goodness of fit to pasture based data. The most robust of the models were the PL, MG, IG and LQ models of which the latter two are simpler in utilising one fewer parameter to achieve the same level of fitness as the PL and MG models. Of the mechanistic models, the BC model achieved an all round better goodness of fit than the others evaluated in this study.

The best of the four selected model in fitting both herd and individual pasture based Holstein-Friesian cow lactation were the MG and LQ models. It is necessary to model the lactation pattern of individual cows as herd modeling *per se* could mask deviations that may indicate problems with individual cows. The important conclusion from this study is that care must be exercised when interpreting the results of evaluating lactation models based on average milk yield data from diverse herds over multiple lactations and seasons and or with few milk yield records. The recommended models for fitting test-day milk yield in pasture-based dairy system are the IG, and LQ models. Further testing of the properties of the LQ model and its application to modelling data from other production systems are necessary in order to fully explore the potential of the model.

Chapter 7. Comparative analysis of models fitting test-day fat, protein and lactose profiles in pasture-based dairy cows

7.1 Summary

In the previous chapter, fourteen lactation functions were evaluated for goodness of fit in describing milk yield data and the subsequent selection and recommendation of four of the functions as the best in pasture-based dairy cows. In this chapter, the top four functions with the best performance were chosen for a more detailed evaluation in fitting fat, protein, lactose and the ratios of fat:protein, fat:lactose and protein:lactose using data from the Victorian Department of Primary Industry's Ellinbank Research Station. The objectives were to compare the predictive accuracy of the models and to determine the most appropriate models for fitting milk constituent yields in this production system. Model goodness of fit was evaluated on the basis of residual mean square error, the magnitude and distribution of residuals and correlations between observed and predicted values.

The modified gamma (MG) and log quadratic (LQ) models always gave the most precise prediction accuracy in all traits with the exception of fat and protein yields where the bi-compartmental (BC) and incomplete gamma (IG) models performed better. All the models gave similar levels of accuracy of predicting the percentage and yields of milk constituents and their ratios. The residual mean square (RMS) of fitting three of the models to 2,138 individual cow fat yields was significantly lower in the MG compared with the IG and LQ models which did not differ. The RMS did not differ between the IG and MG and between the LQ and MG for protein and lactose yields respectively. It was concluded that all the models except the BC, could be used for fitting milk constituent yield profiles under the pasture-based production system.

7.2 Introduction

Cow milk contains about 87.4 % water, 3-5.5% fat, 3-4% protein and other components such as carbohydrates, minerals and vitamins (Whittemore, 1980). Milk composition varies among animal species and within strains, and is influenced by lactation stage and stage of milk removal. Milk fat is often the most variable milk component, while lactose is the least variable (Whittemore 1980, Mepham 1982, Stanton *et al.* 1992). The shift of emphasis in milk payment systems around the world in favour of milk constituents rather than volume *per se*, and the increasing global awareness for healthy dairy products with more protein and less fat, offers incentives for farmers to adopt production practices to improve milk protein content (Lennox *et al.* 1992, Stanton *et al.* 1992). Moreover, the importance of constituent yields in elucidating the metabolic status of the dairy cow justifies modelling constituent yields (Heuer *et al.* 1999). For instance low milk protein may indicate insufficient energy which has been implicated in fertility problems, while a low or high milk fat:protein ratio may indicate sub-acute ruminal acidosis and metabolic conditions such as ketosis, displaced abomasum, ovarian cysts, lameness and mastitis respectively. The knowledge of the milk constituent profile of individual cows can also help farmers in constituting herds that best meet the production target markets for specialised production and attract premium price for dairy products.

An accurate knowledge of the lactation curves of milk and its constituents is useful in management decisions such as the timing and type of supplementation, estimation of total lactation yield from incomplete records and forecasting herd performance on monthly or individual cow basis (Sauvant, 1988). It is also important in decisions about culling of sick animals and identification of genetically superior animals through the evaluation of progeny records. The knowledge of milk composition (in particular, fat:protein and fat:lactose ratios), has been used to indicate energy status and has proven useful for detecting negative energy balance status and the predisposition of affected cows to metabolic conditions such as acidosis, clinical and sub-clinical ketosis (Grieve *et al.* 1986, Steen *et al.* 1996, Heuer 2000). Reist *et al.* 2002 observed that fat:lactose ratio is the most informative trait for estimating energy balance.

Lactose is the major constituent of milk that determines the rate of water secretion into milk which in turn controls the fat and protein contents. Milk lactose content has been

reported to be associated with fertility (Miglior *et al.* 2007). Francisco *et al.* (2003) concluded that lactose percentage seemed a good predictor of days to first and second postpartum ovulation. Buckley *et al.* (2003) found that cows with higher lactose percentage had higher pregnancy rate than those with low percentage lactose, while Reksen *et al.* (2002) demonstrated that higher lactose percentage in the first 8 weeks postpartum was related to early luteal response in second-parity cows.

The profile of milk components follows a similar pattern to that of daily milk yield with an incline to peak followed by a decline to nadir. Consequently, similar lactation functions that previously modeled milk yield successfully have been equally applied to model milk constituent yields provided they are able to take on a convex shape (Wood 1976, Lennox *et al.* 1992, Stanton *et al.* 1992, Silvestre *et al.* 2006). However, lactose requires a function that has the ability to model the decline phase, as no rise to peak is present (Lombaard 2006).

Wood (1967) suggested that the *incomplete gamma* (IG) model could equally be applied to model changes in liveweight, feed intake, milk cell counts and yields of milk constituents. Goodall (1986) fitted seasonally adjusted IG model to milk, and fat percentages, while Wilmink (1987) fitted the exponential function to milk fat and protein yields. In addition to fat and protein yields, Marrant and Gnanasakthy (1989) and Sakul and Boylan (1992) also fitted curves to lactose yields. Mostert *et al.* (2001) and Groenewald and Viljoen (2003) fitted milk and fat yields to the reduced EXP and the IG models respectively. While the IG model provided a satisfactory goodness of fit to the fat and protein contents of milk, it was unable to adequately model the proportion of lactose contained in milk (Sakul and Boylan, 1992).

Although the milk yield curve is reasonably well modelled (see reviews by Beever *et al.* 1991, Swalve *et al.* 1995, Schaeffer 2004), changes in milk constituent yields, especially the lactose content, over the entire lactation, has not been as well modelled (Lombaards (2006). Therefore, the objective of this chapter was to compare the predictive accuracy of four lactation models for fitting fat, protein and lactose profiles in order to determine which models best describe the milk component production patterns of Holstein- Friesian dairy cows under the pasture-based system.

7.3 Materials and methods

7.3.1 Data management

Test-day data on milk fat, protein and lactose percentages and yields as well as ratios of fat:protein, fat:lactose and protein:lactose totalling 29,586 records from 2,684 lactations over an eight year period (1998 to 2005) at the Ellinbank Dairy Research Station, Victoria, Australia, were utilised in this study. The data were edited to exclude lactations <165d or >350d and records with missing milk yields, birth or calving dates. Additional records excluded from the analysis included records of cows with first recorded day in milk from parturition (DIM), 4>DIM<46 and parity >5. Parities >2 were pooled and referred to as parity 3. Only Holstein Friesian cows were included in the final data which consisted of 20,615 records (2,113 lactations). Management practice at Ellinbank was based on spring calving and perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.) pastures, with strategic use of grain supplements during periods of pasture deficit. Test-day classes were based on an average of monthly test-day twice daily milk yields record except the first test-date which comprised days 5-30 post-calving. Milk constituent yields were analysed for each test-day. Summary statistics of herd characteristics are presented in Table 7.1 showed that daily milk, fat and lactose yields increased with parity. Whereas percentage fat tended to increase as parity increased, percentage protein remained similar irrespective of parity while percentage lactose tended to decline with parity.

Table 7.1. Summary statistics of milk, fat, protein, lactose and their ratios of lactating pasture-based cows.

Parity	Trait	Mean	SD	Min	Max	CV	Number of observations
1	Milk (litres)	16.7	4.67	2.90	38.10	27.98	5,753
	%Fat	4.3	0.71	1.30	7.80	16.55	5,957
	%Protein	3.2	0.36	1.00	6.70	11.20	5,957
	% lactose	5.0	0.39	1.77	10.99.0	7.95	5,217
	Fat yield (kg/d)	0.70	0.17	0.14	1.87	24.84	5,753
	Protein yield (kg/d)	0.53	0.14	0.09	1.56	26.67	5,753
	Lactose yield (kg/d)	0.84	0.26	0.15	2.56	31.09	5,013
	Fat:Protein	1.33	0.17	0.53	2.79	12.64	5,753
	Fat:Lactose	0.89	0.17	0.29	1.69	19.18	5,013
	Protein:Lactose	0.65	0.09	0.27	1.18	13.47	5,013
2	Milk (litres)	18.4	5.74	4.30	39.20	31.21	4,503
	%Fat	4.4	0.74	1.50	7.80	16.77	5,957
	%Protein	3.3	0.37	0.90	6.70	11.34	5,957
	% Lactose	4.9	0.35	1.59	10.99	7.13	5,217
	Fat yield (kg/d)	0.79	0.21	0.22	1.82	26.63	4,503
	Protein yield (kg/d)	0.60	0.17	0.15	1.37	28.84	4,503
	Lactose yield (kg/d)	0.89	0.30	0.19	2.01	33.94	3,890
	Fat:Protein	1.34	0.16	0.66	2.22	11.97	4,503
	Fat:Lactose	0.91	0.17	0.49	1.63	18.90	8,890
	Protein:Lactose	0.68	0.09	0.45	1.39	13.76	8,890
	Milk (litres)	20.4	6.86	0.60	47.60	33.69	9,731
	%Fat	4.5	0.77	0.50	12.10	42.86	10,011
	%Protein	3.3	0.38	0.80	6.30	43.35	10,011
	% Lactose	4.8	0.36	1.46	10.13	45.87	8,973
	Fat yield (kg/d)	0.89	0.27	0.02	2.45	30.45	9,731
	Protein yield (kg/d)	0.66	0.20	0.02	1.55	30.73	9,731
	Lactose yield (kg/d)	0.98	0.36	0.03	2.42	36.74	9,731
	Fat:Protein	1.35	0.18	0.14	30.4	13.28	9,731
	Fat:Lactose	0.93	0.18	0.25	3.29	19.48	8,693
	Protein:Lactose	0.69	0.10	0.46	1.57	14.18	8,693

7.3.2 Models

The incomplete gamma (IG), modified gamma (MG), Log quadratic (LQ) and bi-compartmental (BC) models (Table 7.2) previously described and fitted to milk yield data from Tasmania in Chapter 6, were evaluated for goodness of fit in modelling milk constituents emanating from the Ellinbank Research Station, Victoria. The models were fitted to the mean constituent yield profiles referred to as the “*typical*” percentage or yield of fat, protein and lactose and assessed for goodness of fit. Three of the models were then fitted to 2,138 individual cow milk constituent traits.

Table 7.2. The four best functions used to fit the milk constituent profile

Model	Function	Source	N*
BC	$Y_i = ae^{-bt} + ce^{-dt}$	Ferguson and Boston (1993)	3
IG	$Y_i = at^b e^{-ct}$	Wood (1967)	3
LQ	$\text{Log} Y_i = a(b - \text{Log} t)^2 + c$		3
MG	$\text{Log} Y_i = a - bt' + ct'^2 + d/t$	Morant and Gnanasakthy (1989)	4

*N=Number of model parameters

Abbrev = Abbreviation of the models

where $y(t)$ is fat, protein, lactose and their yield ratios (kg/d) or fat, protein and lactose percentages, at time t (days in lactation), a , b , c , d , are parameters that define the scale and shape of the curve, $t' = (\text{DIM} - 150/100)$. In the BC model, parameters b and d represent the rate of cell proliferation and death respectively (see Chapter 3 for background information on the parameters of the various functions).

7.3.3 Statistical analysis

7.3.3.1. Mean (typical) milk components evaluation

All the test-day records were analysed for month in milk (TD) by the *general linear models* (GLM) procedures of the Statistical Analysis Systems Institute (SAS 2002) for unbalanced data to determine the typical curves of the milk constituents as previously defined. The model used was

$$Y_{ijklmn} = \mu + TD_i + CY_j + M_k + PT_l + b(Md_{ijklm} - \overline{Md})^2 + e_{ijklmn} \quad 7.5$$

where Y_{ijklmn} is the $ijklmn$ observation on daily percentages, yields and ratios of fat, protein and lactose; fixed effects of TD_i of i^{th} test-day ($i=1, 2, \dots, 11$), CY_j of j^{th} calving year ($j=1, 2, \dots, 7$), M_k of k^{th} test month ($k=1, 2, \dots, 12$), PT_l of l^{th} parity ($l=1, 2, >2$), with, b as partial regression coefficient of the interval between calving and first test-day recording, $(Md_{ijklm} - \overline{Md})^2$ is the day at first test-day fitted as a covariate, μ is overall mean and e_{ijklmn} is random sampling effect of lactation n with mean zero and variance σ_e^2 . Differences in data sizes between factors included in the model for each region precluded the testing of interaction effects.

The resulting least squares means of the various traits for the eleven TD's provided the average daily values of all the traits in months (1-11) of lactation subsequently referred to as the typical constituents (FY, PY, LY etc) lactation profile. These data were fitted to each of the lactation functions in turn using the Marquardt's iterative method of the

non-linear (NLIN) procedure of SAS (SAS 2002) on lactation stage in days (DIM) using the mid-point equivalent day in milk i.e. 15 for TD1, 45 for TD2 and so on of the respective typical constituent yields.

The models fitted to these curves were compared based on root means square error (RMSE) obtained as the square root of the error mean square (RMS), the magnitude and distribution of residuals and the correlation between observed and predicted traits. Other characteristics of the lactation curve such as peak yield, day at peak, persistency and yield to 305d were either calculated using the relevant formula in the original models or derived from the curve. In order to obtain a uniform and comparable value of persistency across functions, persistency was defined in this thesis as the ratio of the difference in daily constituent trait at day in milk (DIM) 60 and 270 and the number of days during the same period expressed in L⁻³ /d, using the formula

$$P_{\text{lact}} = (Y_{270} - Y_{60}) / 210 \quad 7.6$$

where P_{lact} is the persistency of the respective milk constituent, Y_{270} and Y_{60} is daily constituent trait on DIM 270 and 60 respectively expressed in gram. These days were chosen because for most pasture-based dairy cows, peak milk yield would have been attained before or on day 60 post-partum. Similarly, although lactation length could vary in different production systems, under the pasture-based yearly calving system, most lactations would last 270 days or beyond. Yields to 305d were obtained by summation, after calculating the daily milk constituent trait values for each day of lactation.

The resulting RMS (Table 7.3) of fitting all the functions shown in Table 7.2 to the herd data were used to estimate daily FY, PY and LY on the successive 10th day in lactation i.e. DIM = 10, 20, 30 etc, making up 30 predicted values for each function. The residuals of these estimated values were calculated using the corresponding typical values and residual mean squares (RMS) computed as a measure of goodness of fit using the formula (Pollott and Gootwine 2000):

$$RMS = (\sum_{i=1}^N (M_{\text{pred}} - M_{\text{typ}}))^2 / N - Q \quad 7.7$$

where M_{pred} and M_{typ} were the predicted and actual (typical) values on each of the chosen days, respectively, N was the number of daily F, P or L records in the lactation (in this case 30) and Q was the number of parameters in the model. The resulting RMS were then ranked in order of best to worst goodness of fit of the functions (Table 7.4). Other factors considered in identifying the best fitting model were the number of parameters in the function and the correlation among the parameters.

7.3.3.2. Individual cow milk components evaluation

Based on the goodness of fit of the four tested functions, three best fitting functions were considered for fitness to individual cow milk component traits. These were the IG, MG and LQ functions. These functions were fitted in turn to 20,615 lactations records (2113 cows). Each cow was required to have at least five test-day records. The lactations were grouped according to their mean first recorded test-day or minimum day in milk (MID), maximum day in milk (MXD), number of test-days (NTD) and parity (P). These classes are; MID: (early $5 < \text{MID} \leq 15$, medium $15 < \text{MID} \leq 30$ and late $30 < \text{MID} \leq 45$), MXD: (short $165 < \text{MXD} \leq 270$ and normal $270 \leq \text{MXD} \leq 305$), NTD: (fewer $5 < \text{MID} \leq 7$, Few $7 < \text{MID} \leq 9$ and full $9 < \text{MID} \leq 12$), and P: (1, 2 and >2). These classes contained (728, 961, 424), (1545, 568), (194, 645, 1274), (621, 477 and 1015) individual cows respectively.

The three functions were fitted to the 2113 individual lactations using the iterative non-linear curve fitting procedure, as described above. The RMS's obtained from fitting each function to the lactations were then analysed, using all the functions together and separately for each function. Differences between the goodness of fit of the 3 functions fitted to the individual lactations were investigated using the following model:

$$R_{ij} = LR_i + MOD_j + e_{ij} \quad 7.8$$

where R_{ij} was the RMS derived from fitting the functions to the individual lactation records of F, P, or L, LR_i was the i^{th} lactation record ($i=1 \dots 2113$), MOD_j was the j^{th} model function ($j=1 \dots 3$) as shown in Table 7.7 and e_{ij} was the error term. Differences between the means were tested using the least significant difference (LSD) method. A

least squares procedure fitting a general linear model was used to evaluate the effect of MID, MXD and NTD classes and their interactions on the goodness of fit of each model according to the following model:

$$R_{ijklm} = MID_i + MXD_j + NTD_k + P_l + (MIN)_{ik} + (MXN)_{jk} + b(Y - \bar{Y})^2 + e_{ijklm} \quad 7.9$$

where R_{ijklm} was the RMS derived from fitting a particular function to the individual cow F, P and L yield records, MID_j is the i^{th} minimum test-day, ($i=1 \dots 3$), MXD_j is the j^{th} maximum recorded day in milk ($j=1 \& 2$), NTD_k is the k^{th} number of test-day records ($k=1 \& 2$), Pl is the l^{th} parity ($l=1 \dots 3$), first order interaction effects of $(MIN)_{ik}$ of minimum test-day and number of test-day, first order interaction effects; $(MXN)_{jk}$ of maximum test-day and number of test-days, partial regression coefficients $b(Y - \bar{Y})^2$ of F, P or L yield fitted as covariate and e_{ijklm} is a normally and independently distributed residual effect and e_{ijklm} was a randomly distributed error term. Least squares means, within an effect, were compared and the paired differences between levels within an effect were tested using the least significant difference method.

7.4 Results

7.4.1 The goodness of fit of yields and percentage component yields

The parameter estimates and RMSE values of the models for percentage and yields of F, P and L are presented in Table 7.3. Convergence was achieved in all the models although the BC model did so often with error messages, such as “the model converged but a note in the log indicate errors”. Sometimes the standard errors of parameters or correlations among parameter estimates were not reported. The RMSE for yield traits was highest in the BC and IG models except in FY when the BC model had a lower RMSE than all the other models. The MG and LQ models always produced the lowest RMSE values, except with respect to FY and PY where the BC and IG models respectively had lower RMSE values. Similar trends were observed in the goodness of fit of percentage milk components. The LQ and MG models improved on the goodness of fit of percentage milk components compared to the other two models. All the models generally achieved a good representation of the profile of milk component ratios.

A ranking the goodness of fit of the four models based on the RMS values is shown in Table 7.4. It was obvious that the MG model had the lowest RMS value and was ranked best in representing the FY, PY and LY based on the 30 predicted yields on DIM 10...300 from the typical data. The LQ model gave the best prediction (lowest RMS for %F and %P while the MG again had a lower RMS than the LQ model; for %L). The BC model consistently predicted both of milk component percentage and yield of the typical lactation data least accurately.

7.4.2 Typical lactation curves of percentage, yields and ratios of milk components

The typical lactation curves of percentage, yield (kg/s) and ratio of milk components are shown in Figure 7.1. Fat yield (kg/d) started at 1.00 increased to peak level of 1.16 sixteen days post-partum and declined gradually until lactation end at 0.60. Protein yield was 0.80 the fifth day after calving attained peak level at 0.90 seven days later and declined to 0.44 at the end of lactation, while LY were 1.04, 1.36 and 0.56 at the beginning, peak and end of lactation respectively. On the other hand, %F and %P declined from initial production level reaching nadir points and then increasing towards the end of lactation while %L first reached a peak, from an initial lower level, about 60d post-partum and maintained a relatively constant level throughout lactation. The profile of the FY and LY were similar to that of the %F and %P in that both curves started at a higher level, attained nadir levels and increased to peak at the end of lactation. The profile of the FY and PY ratios on the contrary behaved like the %L curve. The value of the ratio of FY and PY ranged from 1.27 at DIM 21 to 1.50 at DIM 299, compared with 0.82 to 1.09 and 0.60 to 0.79 for the ratio of FY vs. LY and PY vs. LY respectively. The patterns of residual distribution of the %F, %P and %L were generally more random, lower and similar among all the models compared with the residuals of the yield traits. The BC model exhibited positive serial correlations in fitting the ratio of FY:PY.

Table 7.3. Lactation parameter estimates and the root mean square error (RMSE) of the functions fitted to the typical Holstein-Friesian lactation data.

Trait	Model	Typical Holstein-Friesian lactation function	RMSE
Fat Yield (FY)	BC*	$Y_t = 1.0414e^{-0.00297t} + 0.0787e^{0.0037t}$	0.005
	IG	$Y_t = 1.297t^{0.0575}e^{-0.00119t}$	0.014
	LQ	$\text{Log}Y_t = -0.0514(2.6048 - \text{Log}t)^2 + 0.0792$	0.011
	MG	$\text{Log}Y_t = 0.1261 - 0.00285t' + 0.00000356t'^2 - 0.1616/t$	0.008
Protein Yield (PY)	BC*	$Y_t = 2.416e^{-0.0018t} + (-1.603)e^{0.018t}$	0.019
	IG	$Y_t = 1.0123t^{0.067}e^{-0.00116t}$	0.006
	LQ	$\text{Log}Y_t = -0.0503(2.50 - \text{Log}t)^2 - 0.192$	0.008
	MG	$\text{Log}Y_t = -0.1995 - 0.00245t' + 0.00000246t'^2 + 0.610/t$	0.006
Lactose Yield (LY)	BC*	$Y_t = 7.348e^{-0.00224t} + (-6.052)e^{0.0224t}$	0.022
	IG	$Y_t = 1.255t^{0.001}e^{-0.00234t}$	0.023
	LQ	$\text{Log}Y_t = -0.099(3.21 - \text{Log}t)^2 + 0.229$	0.014
	MG	$\text{Log}Y_t = 0.385 - 0.00368t' + 0.00000372t'^2 - 1.95/t$	0.014
% Fat (PF)	BC*	$Y_t = -0.253e^{(-0.0006)t} + 4.305e^{(-0.0006)t}$	0.105
	IG	$Y_t = 4.998t^{-0.060}e^{(-0.0011)t}$	0.037
	LQ	$\text{Log}Y_t = 0.051(3.808 - \text{Log}t)^2 + 1.410$	0.009
	MG	$\text{Log}Y_t = 1.347 - (-0.0080)t' + 0.000000837t'^2 + 1.653/t$	0.006
% Protein	BC*	$Y_t = 6.810e^{(-0.0005)t} + (-3.760)e^{(-0.0005)t}$	0.093
	IG	$Y_t = 3.877t^{-0.069}e^{0.0011t}$	0.041
	LQ	$\text{Log}Y_t = 0.052(3.913 - \text{Log}t)^2 + 1.12$	0.006
	MG	$\text{Log}Y_t = 1.026 - (-0.0010)t' + (-0.000000623)t'^2 + 2.310/t$	0.007
% Lactose	BC*	$Y_t = 10.306e^{0.00008t} + (-5.371)e^{0.00008t}$	0.024
	IG	$Y_t = 4.932t^{0.00017}e^{-0.000079t}$	0.026
	LQ	$\text{Log}Y_t = 0.052(3.913 - \text{Log}t)^2 + 1.12$	0.005
	MG	$\text{Log}Y_t = 1.619 - 0.00032t' + 0.0000007t'^2 + (-0.343)/t$	0.004
Fat :Protein ratio	BC*	$Y_t = 14.15e^{(-0.0001)t} - 12.82e^{(-0.0001)t}$	0.011
	IG	$Y_t = 1.30t^{0.006}e^{(-0.00006)t}$	0.011
	LQ	$\text{Log}Y_t = 0.00096(-.71 - \text{Log}t)^2 + 0.259$	0.008
	MG	$\text{Log}Y_t = 0.324 - (0.0003)t' + 0.000000094t'^2 - 0.696/t$	0.006
Fat :Lactose ratio	BC*	$Y_t = -0.053e^{(-0.0006)t} + 0.899e^{(-0.0006)t}$	0.019
	IG	$Y_t = 0.999t^{-0.048}e^{(-0.00095)t}$	0.011
	LQ	$\text{Log}Y_t = 0.0435(3.78 - \text{Log}t)^2 - 0.157$	0.008
	MG	$\text{Log}Y_t = -0.227 - (-0.0009)t' + (-0.000000419)t'^2 + 1.61/t$	0.009
Protein :Lactose ratio	BC*	$Y_t = -0.779e^{0.0005t} + 1.41e^{0.0005t}$	0.020
	IG	$Y_t = 0.796t^{-0.067}e^{-0.0011t}$	0.010
	LQ	$\text{Log}Y_t = 0.0499(3.919 - \text{Log}t)^2 - 0.456$	0.009
	MG	$\text{Log}Y_t = -0.555 + 0.00011t' + 0.00000083t'^2 + 2.37/t$	0.010

Models are as previously defined in Table 7.2.

* Model converge with errors message

† In the BC model parameters b and d represent the rate of cell proliferation and death respectively

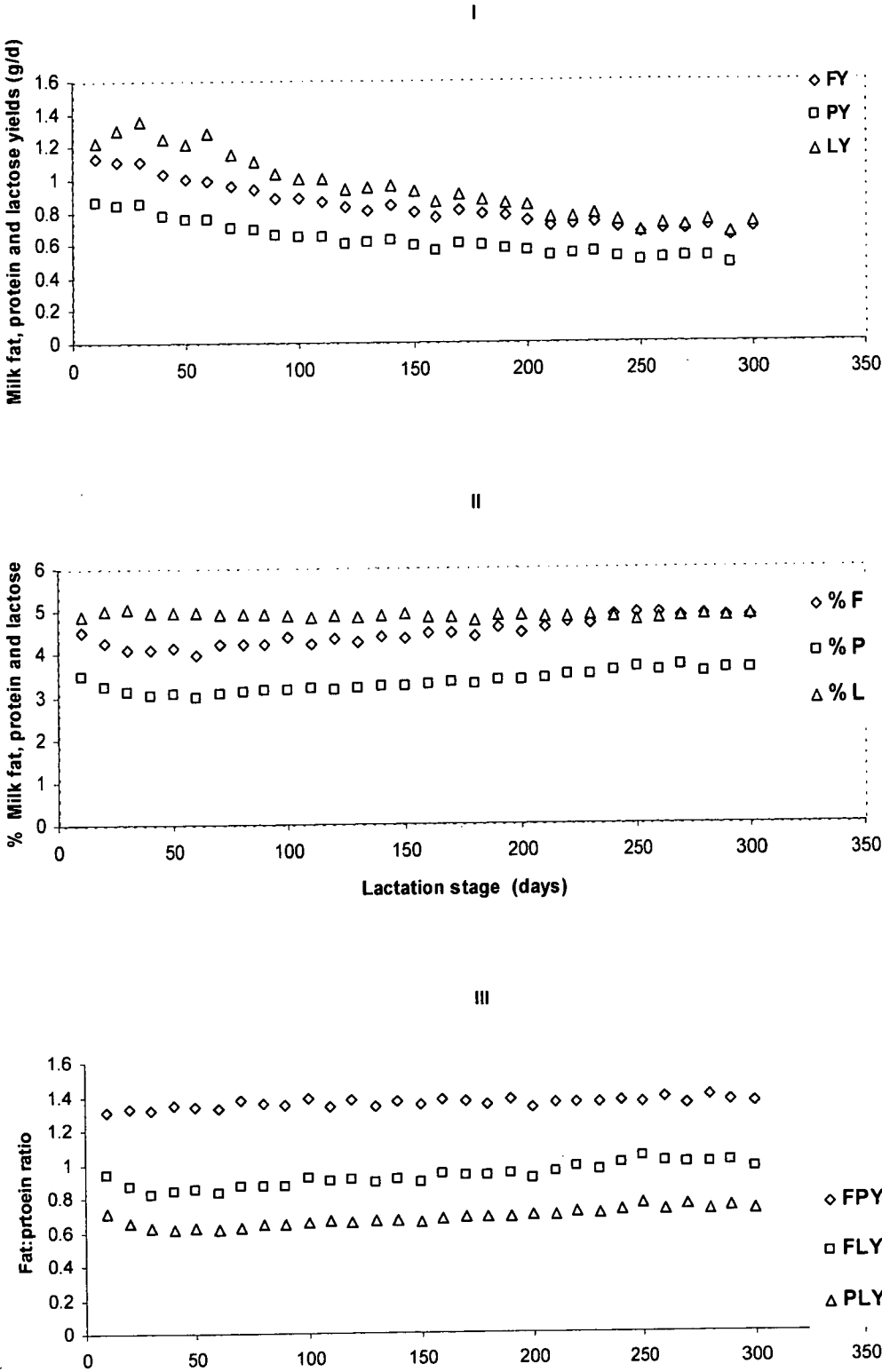


Figure 7.1. The actual yields (I), percentage (II) and ratios (III) of fat, protein and lactose obtained from the least squares means of fitting 20,615 lactation records adjusted for test-day, test-year, test-month, parity and minimum day at first record

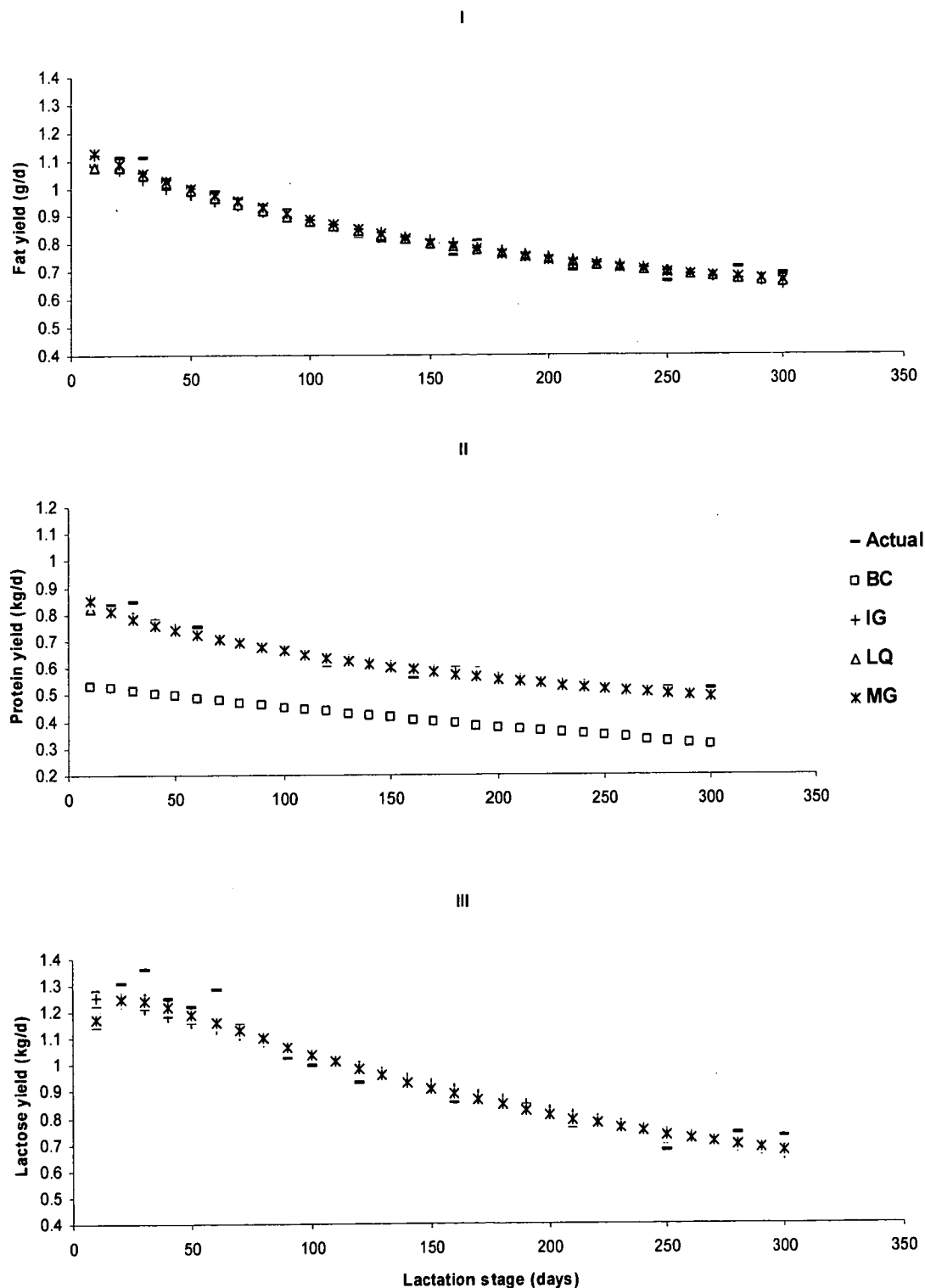


Figure 7.2. Comparison of actual and predicted daily fat (I), protein (II) and lactose (III) yields of Holstein- Friesian cows obtained from fitting the typical lactation data to four lactation functions. Models are: BC = Bicompartmental (Ferguson and Boston 1993), IG= Incomplete *gamma* (Wood 1967), LQ=Log Quadratic and MG =Modified Gamma (Morant and Gnanasakthy 1989)

All the models slightly over-predicted initial FY by an average of 0.12kg/d but the highest error of prediction was observed in the IG and MG models while the lowest error occurred in the LQ model (Figures 7.2 and 7.3 and Table 7.6). The prediction of FY improved in all the models until 100d post-partum when FY was under-predicted in all models. The BC model gave the least accurate representation of PY. Whereas the other models had a mean error of prediction averaging 0.002kg/d the BC model under-predicted PY by an average of 0.21kg/d throughout lactation. All the models accurately represented LY except between 10 to 60d post-partum when all the models equally under-predicted LY.

7.4.3 Parameters of the milk constituents

Estimated parameters of the milk constituent percentages and yields are shown in Table 7.4. All the models over-predicted initial FY, PY and LY yield (Figures 7.2 and 7.3 and Table 7.4). The highest margin of prediction error was obtained from fitting the BC model while the lowest was in the LQ. All the models under-predicted peak FY, PY and LY except the IG and MG models which slightly over-predicted FY and PY respectively. The MG most accurately predicted peak FY while the IG and MG models better fitted the PY. The models did not differ in their accuracy in predicting peak LY. The LQ models achieved the closest goodness of fitness of the %F and %P and all the models equally under-predicted peak of %L by about 0.19. None of the models accurately predicted day at peak milk constituent except the LQ which accurately predicted PY and over-predicted day at peak FY by three days in contrast to the other models which under-predicted FY and PY by as much as 6 and 7 days respectively. On the contrary, the BC and IG models more accurately predicted day at peak of %F and %P while the LQ and MG models better predicted the %L.

All the models over-predicted nadir milk constituent profiles, achieved more accurate prediction of the day at nadir FY, PY and LY and over-predicted day and nadir %F and %P except the BC model which under-predicted PY, %F and %P. The margin of prediction error of FY at day 305 was highest in the MG and lowest in the LQ model. The BC model over-predicted PY to 305d by 61.2kg while the LQ model only over-predicted the same trait by 0.7kg, these being the worst and best predictors of yield to

305d respectively. All the models achieved high goodness of fit or mean percentage constituents and equally under-predicted persistency of milk constituent traits.

Table 7.4. The goodness of fit and ranking(superscripts) of the four models based on the residual means squares obtained from the residual values of the predicted typical lactation data of milk percentage and yields of constituents every tenth day in lactation.

Variables	RMS			
Models	BC	IG	LQ	MG
Fat yield *	24.27 ⁴	7.37 ³	3.43 ²	1.84 ¹
Protein yield *	1.17	4.06	1.87	1.12
Lactose yield *	47.13	14.96	7.95	3.60
% Fat	0.0184 ⁴	0.0092 ³	0.0068 ¹	0.0074 ²
% Protein	0.0132 ⁴	0.0049 ³	0.0028 ¹	0.0031 ²
% Lactose	0.0023 ³	0.0023 ³	0.0021 ²	0.0018 ¹

*The same rankings as milk yield are applicable for Fat, Protein and Lactose yields

Table 7.5. Correlations between actual, predicted and residual fat, protein and lactose yield and percentage values obtained from fitting the typical herd data to four lactation functions.

Variables	Predicted				Residuals			
Actual	BC	IG	LQ	MG	BC	IG	LQ	MG
Models								
Fat yield	0.98	0.98	0.98	0.98	0.39	0.44	0.47	0.20
Protein yield	0.97	0.98	0.98	0.98	0.93	0.39	0.41	0.31
Lactose yield	0.98	0.98	0.98	0.98	0.51	0.51	0.51	0.51
% Fat	0.88	0.96	0.94	0.94	0.55	0.60	0.38	0.40
% protein	0.85	0.97	0.96	0.92	0.65	0.75	0.38	0.21
% lactose	0.64	0.64	0.67	0.66	0.90	0.90	0.89	0.81
Fat:Protein ratio	0.40	0.43	0.43	0.48	0.48	0.85	0.85	0.73
Fat:Lactose ratio	0.86	0.92	0.92	0.91	0.64	0.67	0.55	0.52
Protein:Lactose ratio	0.82	0.94	0.94	0.90	0.72	0.72	0.54	0.35

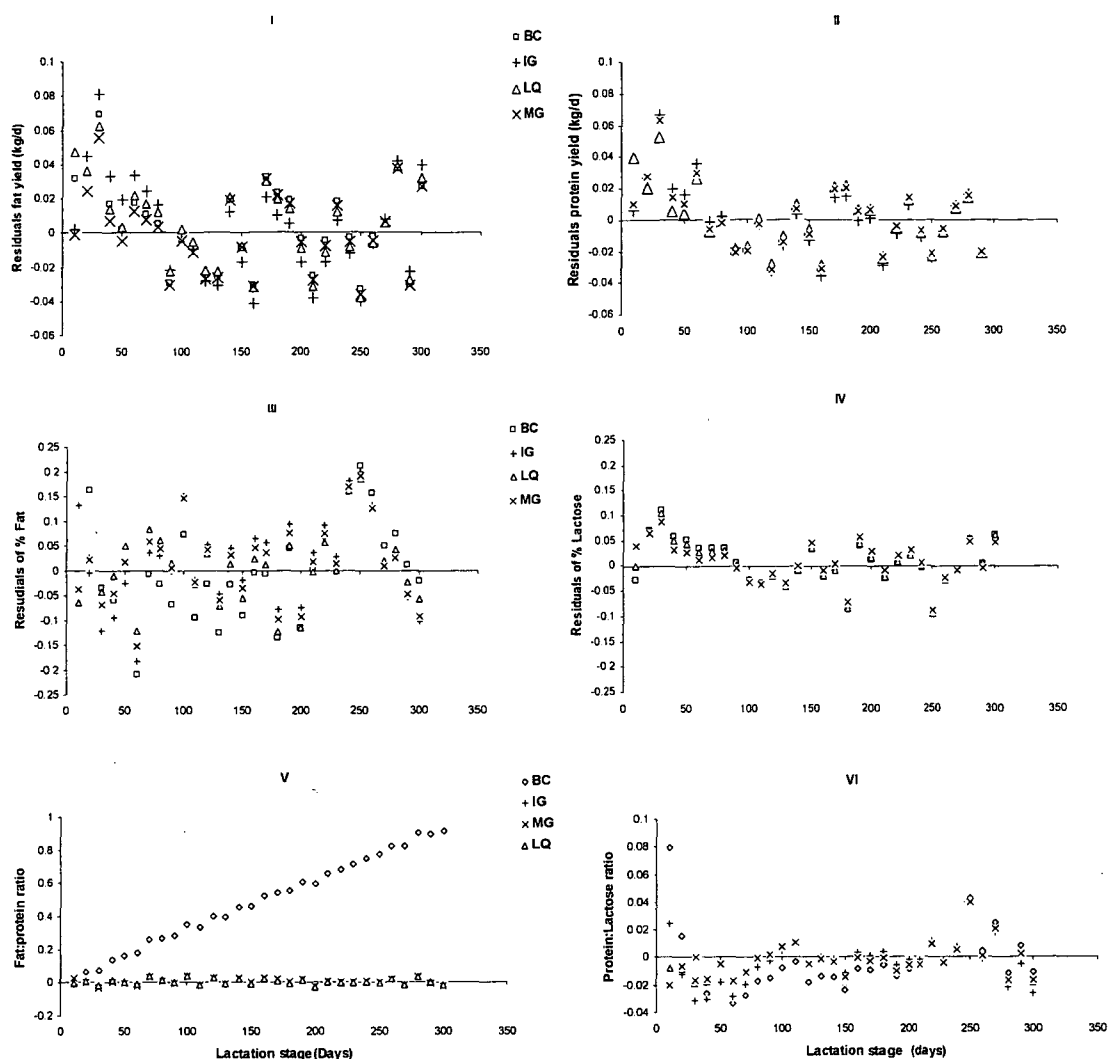


Figure 7.3. Residuals of daily yields, percentages and ratios of fat, protein and lactose from fitting four lactation functions to typical lactation data.

Curves are I=Residuals of fat yield, II= residuals of Protein yield, III=Residuals of % fat and IV= Residuals of %lactose, V=residuals of Fat:Protein ratio and VI=residuals of Protein lactose ratio

Models are \square BC = Bi-compartmental (Ferguson and Boston 1993),

+ IG = Incomplete gamma (Wood 1967)

Δ LQ = Log Quadratic (New model) and

\times MG = Modified gamma (Morant and Gnanaskthy 1989)

Pearson correlations between observed, predicted and residual percentage and yield of milk constituent are presented in Table 7.5. The highest correlation of 0.98 between actual and predicted FY yield was obtained from fitting the all the models to the yield traits. Correlations between actual and predicted percentage fat and protein were lowest in the BC model (0.87) compared to 0.95 for the other models. Correlations between the models for %L, and ratio of FY:PY did not differ. A similar relationship in the

correlations between actual and residuals of the milk constituent traits was observed except for the residual correlations which were generally lower.

7.4.4 Individual cow milk component data

The residual mean squares of the milk component traits and the effects of MID, MXD and NTD are shown in Table 7.7. The mean FY and PY RMS of the 2,113 individual cow lactations were significantly lower ($P<0.05$) in the MG compared to the other two models, but the RMS of FY did not differ between the LQ and the MG models. Minimum day at first test-day did not significantly influence the goodness of fit of the yield traits in all the models except the IG model where goodness of fit was significantly lower when first test-day occurred after 30d post-partum. Lactation length (MXD) significantly ($p<0.05$) improved the goodness of fit of LY in the LQ model when the length of lactation was longer than 270d. The number of test-day records significantly influenced the goodness of fit for FY, PY and LY in all the models, that of PY in the LQ and MG models. The poorest goodness of fit was observed when the number of test days were <7 . Parity influenced the goodness of fit of all yield traits except FY in the IG model. Fat, protein and lactose yields were better predicted in first-parity cows (with the exception of the IG model) than in third-parity cows.

Table 7.6. Comparisons of actual and predicted initial, peak, nadir, 305d cumulative yields, persistency and days to peak and nadir yields and percentages of milk fat, protein and lactose in Holstein-Friesian dairy cows

Trait	Model	Initial	Peak	Peak day	Nadir	Nadir day	305d Yield†	Persistency (g/d)
Fat Yield	Actual	0.99	1.16	11	0.61	266	247.6	1.37
	BC*	1.11	1.11	5	0.66	305	248.7	1.23
	IG	1.14	1.17	5	0.64	305	249.3	1.20
	LQ	1.03	1.08	14	0.66	305	248.6	1.20
	MG	1.16	1.16	5	0.66	305	250.0	1.23
Protein Yield	Actual	0.76	0.91	12	0.44	305	185.7	1.24
	BC*	0.54	0.54	5	0.31	305	124.5	0.74
	IG	0.90	0.90	5	0.48	305	186.8	0.99
	LQ	0.79	0.85	12	0.49	305	186.4	1.03
	MG	0.92	0.92	5	0.49	305	186.7	1.03
Lactose Yield	Actual	1.04	1.36	18	0.56	305	279.9	2.77
	BC*	1.28	1.28	5	0.65	305	280.9	2.02
	IG	1.29	1.26	5	0.65	305	280.9	2.04
	LQ	0.98	1.26	25	0.67	305	280.1	2.14
	MG	0.98	1.26	24	0.67	305	279.9	2.14
Percent Fat	Actual	4.62	5.16	305	3.95	35	4.46‡	-4.05
	BC*	4.06	4.89	305	4.06	5	4.46	-2.78
	IG	4.56	4.98	305	4.17	54	4.46	-3.31
	LQ	5.23	5.23	5	4.10	45	4.47	-3.35
	MG	5.36	5.37	5	4.13	45	4.47	-3.26
Percent Protein	Actual	3.56	3.78	285	3.00	60	3.31	-2.63
	BC*	3.06	3.59	305	3.06	5	3.31	-1.77
	IG	3.49	3.65	305	3.12	63	3.30	-2.02
	LQ	4.03	4.03	5	3.06	50	3.31	-2.28
	MG	4.45	4.45	5	3.07	49	3.32	-2.27
Percent Lactose	Actual	4.97	5.15	59	4.57	194	4.87	0.64
	BC*	4.93	4.93	5	7.82	305	4.88	0.38
	IG	4.93	4.93	5	4.82	305	4.88	0.38
	LQ	4.86	4.93	30	4.82	305	4.88	0.42
	MG	4.71	4.95	35	4.71	5	4.87	0.49

† Fat protein and lactose yields (mg) from DIM 5-305,

‡ mean percentage fat, protein and lactose

* Convergence criteria met with error messages

Table 7.7. Least squares means of the effects of mean daily milk yield (DY), minimum (MID), maximum (MXD) day in milk and number of test-day records (NTD) classes on the residual mean square (RMS) derived from fitting four lactation functions to individual cow lactations.

Factors*	Trait	Fat yield			Protein yield			Lactose yield		
	Factors*									
	Levels*	IG	LQ	MG	IG	LQ	MG	IG	LQ	MG
Model		0.032 ^a	0.029 ^a	0.024 ^b	0.022 ^b	0.029 ^a	0.021 ^b	0.035 ^a	0.026 ^b	0.021 ^b
RMS‡										
SED			0.0019			0.0014			0.0023	
MID	Early	0.040 ^b	0.031	0.025	0.035 ^c	0.026	0.021	0.047 ^b	0.025	0.019
	Medium	0.050 ^b	0.030	0.024	0.067 ^a	0.028	0.020	0.062 ^b	0.025	0.020
	Late	0.082 ^a	0.025	0.001	0.043 ^b	0.025	0.020	0.097 ^a	0.023	0.019
SED		0.006	0.003	0.002	0.006	0.003	0.020	0.007	0.003	0.002
MXD	Normal	0.054	0.029	0.023	0.048	0.026	0.020	0.063	0.020 ^b	0.017
	Short	0.061	0.029	0.023	0.049	0.026	0.023	0.074	0.028 ^a	0.021
SED		0.006	0.003	0.002	0.004	0.002	0.001	0.007	0.003	0.002
NTD	Few	0.025 ^b	0.024 ^b	0.020 ^b	0.013 ^b	0.021	0.017	0.020 ^c	0.019 ^b	0.017 ^b
	Fewer	0.115 ^a	0.036 ^a	0.028 ^a	0.116 ^a	0.031	0.020	0.146 ^a	0.025 ^b	0.018 ^b
	Full	0.033 ^b	0.026 ^b	0.022 ^b	0.017 ^b	0.025	0.022	0.040 ^b	0.030 ^a	0.023 ^a
SED		0.007	0.003	0.002	0.005	0.003	0.002	0.009	0.003	0.002
Parity	1	0.055	0.019 ^b	0.018 ^b	0.055 ^a	0.021 ^b	0.018 ^b	0.089 ^a	0.020 ^b	0.018 ^b
	2	0.057	0.024 ^b	0.020 ^b	0.044 ^b	0.023 ^b	0.017 ^b	0.059 ^b	0.02 ^b	0.017 ^b
	3	0.060	0.043 ^a	0.032 ^a	0.048 ^a	0.033 ^a	0.025 ^a	0.060 ^b	0.032 ^a	0.023 ^a
SED		0.006	0.002	0.012	0.004	0.003	0.002	0.007	0.003	0.002

‡a,b,c Model RMS of entire 2113 individual lactations. Group least squares means in the same row with the same superscript are not significantly different.

*Models are IG=Incomplete gamma (Wood 1967), LQ=Log quadratic (New model) and MG = Modified gamma (Morant and Gnanasakthy (1989) with 3, 3 and 4 parameters respectively.

*Values in the mean RMS column with the same superscript are not significantly different.

7.5 Discussion

In this chapter four of the best performing lactation functions were utilised in fitting percentage and yields of milk constituent data from pasture-based dairy systems. A comparison of their predictive characteristics enables the identification of the most suitable mathematical model for adequately describing both herd and individual cow milk constituent profiles. It also provides a better perspective of the prevailing factors affecting the goodness of fit of the functions. An accurate knowledge of the lactation curves is therefore relevant to management and research in dairy production systems for the timing feed supplementation, estimating total lactation yield from incomplete

records and forecasting herd performance on monthly or individual cow basis (Sauvant, 1988).

Although the goodness of fit as determined by RMSE of the different models differed slightly between and within traits and models in all but the BC function, the performance of the models was generally satisfactory. The MG model achieved the closest prediction to the actual values at the cost of an additional parameter. All the models were generally more robust (except the BC), gave the least RMSE, achieved a more random distribution of residuals and resulted in the highest correlations between actual and predicted data. The poor performance of the mechanistic model (BC) is at variance with the findings of Dijkstra *et al.* (1997), Pollot and Gootwine (2000), who reported that mechanistic models gave better goodness of fit compared with empirical models. However, the similar model performances as reported in this thesis, is in agreement with the reported percentage MY FY and PY (Keown *et al.* 1986) and other milk component yield traits reported by Sylvestre *et al.* (2006).

The suitability of different models reported in the literature has been diverse. For instance, Wood (1976) reported that the IG was suitable for evaluating milk constituent yield. Morant and Gnanasakthy (1989) and Lennox *et al.* (1992) obtained better goodness of fits to milk constituents yield data using the modified IG model of Morant Gnanasakthy (1989) and Goodall (1983), while Cappio-Borlino *et al.* (1995) applied the test-day models for milk constituent evaluation and obtained results that corroborate the findings in this study.

The main difference in the pattern of the predicted values among the four models occurred in the way early lactation records were fitted. The LQ and MG models surpassed both IG and BC models in better representing the early lactation data of the milk constituents. Nearly all the models achieved better goodness of fit after the peak or ebb point of the constituent traits. Stanton *et al.* (1992) opined that the extent to how well a model fitted the yields of milk constituents was determined mostly by the fitness of early lactation, this being the period in which milk constituents, especially FY and PY are most variable (Hurley 2003). Whittemore (1980) noted that colostrum contained twice the normal concentration of solids, five times the protein, approximately twice the

fat and half the lactose. The pattern of production (Figures 7.1 and 72) clearly indicated that milk constituents yield were higher in early, and lower in, late lactations.

Poor goodness of fits in models has also been attributed to insufficient test-day records during early lactation (Pollott and Gootwine 2000), variation between cows (Olori *et al.* 1999), parity (Tekerli *et al.* 2000), pregnancy or health (Wood 1969, Olori *et al.* 1999), irregular record pattern between adjacent test days (Kolver and Muller 1998, Sylvestre *et al.* 2006) and the mathematical property of the model (Macciotta *et al.* 2005). Therefore, the poor goodness of fit of the BC model may therefore be seen in this light. It is possible that mechanistic models require more data points. Dijkstra *et al.* (1997) had reported poor goodness of fits of the Dijkstra mechanistic model when the number of observations was few. Similarly, the study by Pollott and Gootwine (2000) that used weekly test-day records consisting of an average of 42 data point per sheep observed the same scenario of poor fits. Test-day monthly records have become necessary in dairy systems in order to reduce the costs of supervised herd recording for genetic data evaluation. Widespread adoption of automatic milking system with on-line data logging should make more records available for further testing of the robustness of mechanistic models on dairy cows data.

The hypothesis of no significant difference due to insufficient data in early lactation was tested in this study by evaluating the effect of some data properties on the goodness of fit of the four lactation functions. The lack of significant influence of day at first test-day on the goodness of fit of the models in this study was probably due to the availability of early first test-day records within the first 30d post-partum in 80% of the individual cows' records. However, the better performance of the LQ and MG compared with the IG model may be an indication of the former's robustness, due to their mathematical properties or stochastic assumptions. Both LQ and MG models are polynomial models whereas the IG model is an incomplete gamma function with exponential component to represent the decline phase of lactation.

The effect of parity on the goodness of fit of the models is a consequence of the physiological differences between cows of different parities. Lactation curve profiles in first parity cows tend to have lower peaks and higher persistency than higher parity

cows. This difference is attributed to the preferential partitioning of energy into body weight gains, in first parity, as against milk yield in higher parity cows. In this sense, the result in this study is in agreement with the findings of Olori *et al.* (1999), Tekerli *et al.* (2000) and Macciotta *et al.* (2006) which demonstrated that parity and/or age at calving has significant effects on the goodness of fit of curve types in both standard and atypical lactations.

The profiles of milk FY, PY and LY obtained in this study were also similar to the reported profiles of these constituents (Tekerli *et al.* 2000, Hurley 2003, Macciotta *et al.* 2005, Silvestre *et al.* 2006). The fat and protein percentages reported in this study were higher than the values reported by Lennox *et al.* (1999) and Stanton *et al.* (1992). The difference is attributable to genetic gains achieved through sustained selection for increased milk yield in dairy cows in the last two decades (Peyraud and Delaby 2001) as well as improvement in management practices especially in increasing the proportion of grain concentrates in the diets of pasture-based dairy cows in Australia (FAO 2007).

The inaccurate estimation of milk component yields at various lactation stages observed in this study conform to the well reported limitations of empirical models (Wilmink 1987, Olori *et al.* 1999). Although the BC model attained convergence, the poor goodness of fit to the data was well reflected in the higher RMS and distribution of residuals with respect to lactose percentage (Table 7.3).

7.6 Conclusion:

The results herein indicate that all the models except the BC are capable of adequately representing the lactation profile of milk component traits. Desirable as it was to find a mechanistic model capable of fitting milk constituent percentage and yield data from the prevailing dairy system in Tasmania, the results of fitting the BC model, which was the best fitting mechanistic model to milk yield in Chapter 6 was not satisfactory. The best overall models for fitting either herd or individual cow milk composition data were the MG and LQ models. Both models showed robustness, fitted the data with lower RMSE and attained similar levels of goodness of fit. However, the LQ model has the advantage of being simple and parsimonious in having only three parameters. This result provides information which may serve as a basis for the evaluation of milk constituent profiles of

herd and individual cows in similar production systems. It also opens the prospect to explore the application of the of the LQ model for fitting lactation data to a wider national database. Prospects for future studies would be the evaluation of genetic parameters of this model as well its use in estimating breeding values of dairy cows.

Evaluation of goodness of fit of fifteen lactation curves in chapter six led to the identification of four parametric models which achieved high goodness of fit to daily milk yield data and have now been successfully fitted to milk constituent yield profiles. The models have demonstrated robustness in fitting both herd and individual cow's lactation and the least square means method also enabled the testing of some effects of data sampling properties on the goodness of fit of the models. The advantage of parametric models is that they provide parameters that may be related to physical components of the lactation. In order to account for the environmental perturbations affecting milk and milk component traits on each test-day when dealing with hierarchical time series data the parametric models have limitations. The next chapter of this thesis will explore the use of random regression models in partitioning the variation due to each test-day into fixed and random effects and how these affect curve shapes.

Chapter 8. Factors affecting the shapes of lactation curves in pasture-based Holstein-Friesian cows

8.1 Summary

Various lactation functions were fitted to test-day data emanating from herd group and individual cows in the preceding chapters. Four functions with the best goodness of fit were deemed to be the most suitable for modelling lactation in pasture-based dairy systems (Chapters 6 and 7). It was also demonstrated that large goodness of fit variations existed between functions derived from individual cow data compared to herd group data. However, the limited exploration of the factors affecting the goodness of fit of the models presents a knowledge gap that this chapter attempts to fill. Therefore, as a logical progression of thoughts, the objective of this chapter was to further explore and investigate the factors affecting the shapes of lactation curves. The output, parameter estimates a , b and c (obtained from fitting the IG and LQ models to individual cow test-day data) and environmental/management factors were utilised. The data comprised of 76,762 lactation records of 8,441 dairy cows from 126 herds in four Tasmanian dairy regions collected between 2005 and 2007. It was evident that the parameters of both models were significantly influenced by physiological, environmental and management factors. The heritability of parameter a was highest being 0.26 (IG) and 0.20 (LQ). The heritability of all parameter estimates ranged from 0.16 to 0.26 but heritabilities were lower for other lactation traits possibly due to the comparatively limited data size occasioned by missing pedigree information of some cows in the data use in this study. Phenotypic and genetic correlations were consistent with reported values in the literature and did suggest that the parameters of the models could be used to genetically influence the lactation profile.

8.2 Introduction

The profitability of the dairy enterprise is in part, influenced by genetic and phenotypic factors which affect milk yield and productive lifespan of the lactating cow. Some of these factors include breed, sire genetic merit, production potential, parity, hormones, lactation stage, age and body weight at calving, gestation, dry period, season, disease occurrence and plane of nutrition (Danell, 1982). Factors affecting total milk yield do not only influence the daily milk yield, but also the parameters of test-day milk yield (Ray *et al.* 1992; Tekerli *et al.* 2000, Macciotta *et al.* 2005). Factors known to influence lactation curve shapes are cow breed (Shanks *et al.* 1981; Grossman *et al.*, 1986), fixed environmental factors (Tozer and Huffaker 1999, Rekik and Gara 2004), and management practices (Tekerli *et al.* 2000, Val Arreola *et al.* 2004).

Milk yield to 305 days is often used in animal genetic evaluations and other management decisions. However, the quest for early predictors of milk yield led to the development of lactation functions (Wood 1967, Cobby and Le Du 1978, Wilmink 1987) that assist in summarising the lactation profile into biologically interpretable parameters. The incomplete gamma function is the most often used function to model lactation (Olori *et al.* 1999, Tekerli *et al.* 2000; Silvestre *et al.* 2006) and explore the factors affecting its three parameters which are related to the initial milk yield, the incline to peak and decline phases respectively. The resulting parameter estimates from these functions can be further analysed to estimate systematic effects, predict future yields from incomplete lactation records and detect deviation of an individual cow or a herd of cows from the expected performance. They also provide early estimates of 305-day milk yield, persistency and peak milk yield (Jensen 2001, Schaeffer 2004) since peak yield is highly correlated to total milk yield (Gengler, 1996)

Although lactation curve studies deal with average patterns of homogeneous groups of animals, individual animal curves are of practical interest for cow health monitoring, feeding and genetic evaluations. Individual curve fitting in dairy cows results in a wide range of goodness of fit, due to the large random variation of shapes among animals (Olori *et al.* 1999), environmental perturbations (Rekik and Ben Gara 2004) or the mathematical

properties of the function (Landete-Castillejos and Gallego 2000, Macciotta *et al.* 2005). As a follow up to the identification of the best four lactation functions for fitting data from pasture-based dairy systems, the objective of this chapter was to determine the environmental and management factors affecting the shapes of lactation curves using the IG and LQ models. The second objective was to evaluate the genetic parameters of both models.

8.3 Material and methods

8.3.1 Data management

The data used in this study comprised of the parameter estimates (a , b and c), obtained from fitting the IG and LQ models to individual cow test-day data. These parameters were merged with the respective environmental or management factors on 76,762 lactations records of 8,441 cows from 126 dairy herds in four Tasmanian dairy regions over a three-year period (2005–2007). Data editing details had already been presented in Chapter 6 and will therefore not be over-laboured herein. To test the effects of various non-genetic factors on curve shapes, all parameter estimates of the *atypical* lactations i.e. lactations with negative parameters b and c (IG model), positive parameter a and negative parameters b and c (LQ model) were then excluded from the analysis. This is because according to Rekik and Ben Gara (2004), their inclusion can lead to computational difficulties in estimating other parameters such as peak yield, time to peak and total milk yield of the IG model. Furthermore, comparative analyses of factors affecting curve shapes are better done among homogeneous curves (Macciotta *et al.* 2005). The final data sets consisted of 5,599 and 6,908 individual lactations with respect to the IG and LQ data, respectively. Summary statistics of mean parameter estimates of both models are shown in Table 8.1.

Chapter 8. Factors affecting the shapes of lactation curves in pasture-based Holstein-Friesian cows

Table 8.1. Summary statistics of the main lactation parameters of the two models

Model	Factors	Parameters*								
		A			B			c		
		Mean	SD	N	Mean	SD	N	Mean	SD	N
IG	Parity									
	1	6.03	3.880	1302	0.32	0.227	1302	0.01	0.003	1302
	2	8.64	5.311	1239	0.28	0.209	1239	0.01	0.003	1239
	3	9.33	5.921	3056	0.30	0.241	3056	0.01	0.003	3056
	Calving season									
	Autumn	7.77	5.695	677	0.30	0.275	677	0.00	0.003	677
	Spring	9.64	5.476	2355	0.26	0.208	2355	0.01	0.003	2355
	Summer	10.19	5.659	28	0.19	0.162	28	0.00	0.002	28
	Winter	7.42	5.322	2537	0.33	0.234	2537	0.01	0.003	2537
	Calving year									
	2005	7.98	5.552	142	0.33	0.241	142	0.01	0.003	142
	2006	10.56	7.190	386	0.26	0.221	386	0.00	0.003	386
	2007	8.26	5.357	5069	0.30	0.231	5069	0.01	0.003	5069
LQ	Parity									
	1	-0.20	0.138	1611	3.77	1.011	1611	2.57	0.267	1611
	2	-0.20	0.133	1487	3.60	1.224	1487	2.82	0.294	1487
	3	-0.21	0.149	3809	3.55	2.620	3809	2.92	0.281	3809
	Calving season									
	Autumn	-0.17	0.147	817	4.25	5.595	817	2.71	0.380	817
	Spring	-0.18	0.126	2920	3.36	0.786	2920	2.87	0.295	2920
	Summer	-0.10	0.080	44	3.91	3.914	44	2.87	0.368	44
	Winter	-0.25	0.149	3126	3.68	0.697	3126	2.79	0.301	3126
	Calving year									
	2005	-0.24	0.191	181	3.69	0.921	181	2.84	0.356	181
	2006	-0.18	0.136	484	3.83	6.914	484	2.92	0.370	484
	2007	-0.21	0.142	6242	3.60	1.043	6242	2.81	0.306	6242

*Parameters of the LQ model are in Log_e

Models are Incomplete gamma (IG) $Y_i = at^b e^{-ct}$ and Log Quadratic (LQ) $\text{Log} Y_i = a(b - \text{Log} t)^2 + c$

Other characteristics of the lactation curve such as the peak milk yield (PY), day at peak milk yield (DP) and persistency of the lactation were calculated for each function using the formula proposed by Wood (1967) for the IG model and other equations previously proposed in Chapter 6. Persistency of lactation for the LQ function was defined as the ratio of the difference in daily milk yield at DIM 60 and 270 and the number of days during the same period expressed in mL/d (see Chapter 6). Cows with lower values were more persistent than those with higher values.

8.3.2 Statistical analysis

The edited data files for both models were first analysed using univariate mixed models in ASReml (Gilmour *et al.* 2006) to obtain start-up values for the covariance structures in subsequent analyses. Parity (P), Calving year (Y), calving season (S), and their first order interactions (YS), and herd x calving year interaction (HY) were the fixed effects while individual cow was used as a random effect. Average daily milk yield was included in the model as a covariate. A single multivariate analysis was performed to estimate the effects of environmental and management factors, genetic parameters (heritabilities, phenotypic (r_p) and genetic (r_g) correlations) among the three parameter estimates of the lactation curve namely parameters a , b and c , while univariate analyses were performed on the other lactation traits such as peak milk yield, persistency and day at peak yield. The full model was

Each of the data sets was fitted in turn to the model which has the form;

$$y_{ijklmn} = \mu_i + Y_{ik} + P_{il} + S_{im} + YS_{ikm} + HY_{in} + \beta mk + a_{ij} + e_{ijklm} \quad 8.2$$

where i represent the parameters a , b , c (fitted as multivariate), lactation persistency, peak milk yield and day at peak milk yield, μ_i is the population mean for parameter i , y_{ijklmn} is the observation of parameter i for cow j , Y_{ik} , P_{il} , S_{im} , YS_{ikm} , and HY_{in} are the fixed effects of the parameters on k^{th} calving year ($k=1,2$ and 3), l^{th} parity ($l=1,2$ and >2), m^{th} calving season $m=(1,2,...4)$, ikm^{th} first order interaction of calving year and season ($ikm=1,2,...12$), and in^{th} herd-year interaction ($in=1,2,...360$), respectively, β is the regression coefficients of average daily milk yield (mk) on parameter i , a_{ij} is the random additive genetic effect on parameter i for animal j and e_{ij} is the random residual error of parameter i for individual cow j . A pedigree file tracing ancestry to the last five generations was included in the genetic analysis.

In matrix notation the model can be written as

$$y = Xb + Za + e, \quad 8.3$$

where \mathbf{b} includes the fixed effects Y_{ik} , P_{il} , S_{im} , YS_{ikm} , and HY_{iq} , \mathbf{a} is the random animal effect a_{ij} , \mathbf{e} is the vector of random residual effects, and \mathbf{X} and \mathbf{Z} are the incidence and co-variable matrices. Assume that

$$\mathbf{y}|\mathbf{b},\mathbf{a}, \sigma_e^2 \sim N(\mathbf{Xb} + \mathbf{Za}, \mathbf{R}),$$

and

$$\begin{pmatrix} \mathbf{a} \\ \mathbf{p} \end{pmatrix} \sim N(\mathbf{0}, \mathbf{V})$$

with

$$\begin{pmatrix} \mathbf{G} \otimes \mathbf{A} & \mathbf{0} \\ \mathbf{0} & \sigma_p^2 \end{pmatrix}$$

where \mathbf{G} is the covariance matrix of the additive genetic coefficients of the traits assumed to be the same for all cows; \mathbf{A} is the additive genetic relationship matrix among the animals; \otimes is the Kronecker product function (Searle 1982). An unstructured covariance matrix was fitted to the residuals of the mixed models.

The mixed model equation for this model would be

$$\begin{pmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{W} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z} + \mathbf{G}^{-1} \otimes \mathbf{A}^{-1} & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{W} \end{pmatrix} \begin{pmatrix} \hat{\mathbf{b}} \\ \hat{\mathbf{a}} \end{pmatrix} = \begin{pmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{y} \end{pmatrix} \quad (4.4)$$

where \mathbf{G} =additive genetic matrix

8.4 Results

8.4.1 Curve shapes

The two functions described both the standard (*typical*) and non-standard or (*atypical*) lactation curve shapes. The frequency distribution of the different types of curve shapes is shown in Table 8.2. The IG model fitted the *typical* curve shape to 66.3% of the individual cow lactations while the LQ model fitted 81.8% of the curves as *typical*. The number of non-distinct type or poorly fitted lactation is also higher in the IG model being 164 compared with two in the LQ model (Table 8.2).

Table 8.2. Frequency distribution of different lactation curve shapes determined by fitting 8,441 individual cow lactation data to IG and LQ functions

Model parameter	a	b	c	Frequency	Curve Type
IG	+	+	+	5598	Standard or Declining
	+	+	-	28	Continuously increasing
	+	-	-	1140	Decline to nadir followed by incline or continuously increasing
	+	-	+	1447	Continuously increasing or straight line
	-	-	+	15	Straight line followed by decline ("Cliff")
	-	-	-	49	Incline to peak "plateau" and decline
	*			164	
Total				8441	
LQ	-	+	+	6905	Standard
	-	-	+	868	Continuously declining
	+	+	+	610	Decline to nadir followed by incline or continuously declining
	+	+	-	35	Continuously declining
	+	-	-	12	Continuously increasing
	+	-	+	9	Continuously increasing
	*			2	
Total				8441	

*Undefined curve type parameters too small or too large

Figures 8.1 and 8.2 show plots of the different lactation curve shapes for the IG and LQ models respectively, with the corresponding values of the parameter estimates. Both models also showed slight differences in the curve types. Within the standard curve type, the IG model presented two forms, a curve rising to the peak before decline or a continuously declining curve (Figure 8.1 curves I and II). No such dual shapes due to the magnitude of the parameters were observed in the standard curves of the LQ model.

Table 8.3 Predicted parameters a, b, c and linear regression coefficients of lactation curve traits of pasture-based Holstein-Friesian cows

Factors	Model		Log Quadratic						Incomplete Gamma					
	Parameters	Level	a	b	c	persist	Peak yield	Peak day	a	b	c	persist	Peak yield	Peak day
Parity		1	0.864 ^a	35.30 ^a	14.76 ^c	22.48 ^c	15.61 ^c	45.93 ^a	8.62 ^c	0.240 ^b	0.004 ^b	7.13 ^a	15.26 ^c	64.46 ^a
		2	0.846 ^b	31.44 ^b	16.09 ^b	28.74 ^b	16.59 ^b	41.16 ^b	9.09 ^a	0.259 ^b	0.005 ^a	6.94 ^b	16.04 ^b	55.66 ^b
		3	0.822 ^c	31.27 ^c	16.76 ^a	33.08 ^a	17.3 ^a	40.86 ^b	8.75 ^b	0.281 ^a	0.005 ^a	6.93 ^b	16.59 ^a	54.58 ^b
	SED		0.0090	0.051	0.012	0.524	0.081	0.752	0.402	0.0185	0.0002	0.027	0.064	1.027
Calving year		2005	0.842	31.22 ^c	15.83 ^b	26.81	16.23	41.88 ^b	8.32 ^b	0.245 ^b	0.004 ^b	7.02	15.84 ^b	56.17 ^b
		2006	0.845	33.49 ^a	16.07 ^a	28.72	16.76	41.36 ^b	9.65 ^a	0.251 ^b	0.005 ^a	6.93	16.19 ^a	57.06 ^b
		2007	0.834	33.28 ^b	15.65 ^c	28.77	16.51	44.7 ^a	8.47 ^b	0.277 ^a	0.005 ^a	7.05	15.85 ^b	61.47 ^a
	SED		0.0121	0.072	0.013	1.903	0.322	2.801	0.746	0.0337	0.0004	0.105	0.27	4
Calving Season		Autumn	0.858 ^b	46.39 ^a	14.51 ^c	18.1	15.01 ^c	53.73 ^a	7.63 ^c	0.246 ^b	0.006 ^b	7.39 ^a	14.85 ^c	76.81 ^a
		Spring	0.836 ^b	26.15 ^c	16.46 ^a	34.73	17.41 ^a	35.86 ^c	9.63 ^a	0.246 ^b	0.006 ^a	6.72 ^c	16.67 ^a	45.47 ^d
		Summer	0.880 ^a	25.98 ^d	15.88 ^b	23.68	16.33 ^b	40.57 ^b	9.67 ^a	0.205 ^c	0.004 ^b	7.07 ^b	15.55 ^b	61.52 ^b
		winter	0.790 ^c	36.07 ^b	16.63 ^a	35.89	17.25 ^a	40.43 ^b	8.33 ^b	0.309 ^a	0.006 ^a	7.39 ^a	16.77 ^a	49.12 ^c
	SED		0.0144	0.078	0.016	1.582	0.252	2.356	0.665	0.0295	0.0003	0.094	0.221	3.626

Table 8.4. The effect of the calving year and season interaction on the parameter estimates of the incomplete gamma and Log quadratic functions obtained from multivariate analysis of lactation parameters *a*, *b* and *c*.

Model	cavyr	CavSean	a	b	c
LQ	2005	Autumn	0.867	44.36 ^a	14.49 ^c
		Winter	0.802	34.49 ^b	16.62 ^a
		Spring	0.851	24.98 ^c	16.44 ^a
		Summer	0.892	24.85 ^c	15.87 ^b
		SED	0.0896	0.484	0.096
	2006	Autumn	0.859 ^a	47.59 ^a	14.71 ^c
		Winter	0.795 ^b	37.00 ^b	16.87 ^a
		Spring	0.843 ^a	26.80 ^c	16.69 ^a
		Summer	0.884 ^a	26.65 ^c	16.11 ^b
		SED	0.0481	0.260	0.051
	2007	Autumn	0.848	47.29 ^a	14.31 ^c
		Winter	0.785	36.77 ^b	16.41 ^a
		Spring	0.833	26.63 ^c	16.24 ^a
		Summer	0.873	26.49 ^c	15.67 ^b
		SED	0.0403	0.216	0.043
IG	2005	Autumn	7.14	0.257 ^a	0.003
		Spring	9.14	0.233 ^b	0.005
		Winter	7.84	0.296 ^a	0.005
		Summer	9.18	0.192 ^c	0.003
		SED	3.750	0.1705	0.002
	2006	Autumn	8.46 ^b	0.263	0.003 ^b
		Spring	10.46 ^a	0.239	0.006 ^a
		Winter	9.17 ^b	0.302	0.006 ^a
		Summer	10.50 ^a	0.198	0.004 ^b
		SED	2.033	0.0920	0.0011
	2007	Autumn	7.29 ^b	0.290	0.004 ^b
		Spring	9.29 ^a	0.265	0.006 ^a
		Winter	7.99 ^b	0.329	0.006 ^a
		Summer	9.33 ^a	0.224	0.004 ^b
		SED	1.705	0.0770	0.0009

Variation in curve shapes due to differences in the magnitude of the parameters estimates of the IG model were also observed in the non-standard curves types (Figure 8.1 curves V vs. VI and VII vs. VIII). The IG model tended to reflect dual shapes among the *atypical* curves with parameters having the same signs being either continuously increasing or declining to nadir before an ascent. The LQ model on the other hand tended to fit the different *atypical* curve types as either continuously declining or declining to nadir before an ascent. Although the size and sign of the parameters did not dramatically influence the LQ model's *atypical* curve shape, the time at inflection point seemed to affect the shape as shown in (Figure 8.2 curves I vs. II, and V vs. VI).

8.4.2 Factors affecting the shape of lactation curves

The predicted values of the lactation parameter estimates of both models and the factors affecting them obtained from multivariate analysis are shown in Table 8.3. All the tested factors except calving year (parameters a and peak milk yield) in the LQ model and lactation persistency (both models) significantly ($P < 0.05$) influenced curve shapes. Multivariate analysis of the model parameters (not shown in Tables) revealed that physiological factors namely, parity and average daily milk yield (as reflected in the F-value) accounted for the greatest variation in the values of parameters a and b (IG model), whereas environmental factors (calving season and year) explained more of variation in both parameters in the LQ model. Both functions were similar in the proportion of variance explaining parameters a and c . On the other hand, parity and average daily milk yield accounted for the greatest variation in the values of parameters b and c (LQ model) compared with IG model in which calving season explained more variation of both parameters.

Physiological factors

Parameter a was lowest in third and later compared with first and second parity cows (LQ) (Table 8.3). The initial milk yield was significantly higher ($P < 0.01$) in second compared to other parity cows (IG function). In both models, cows in their third and later parities attained higher peak milk yield levels than first and second parity cows. Similarly, first parity cows attained day at peak later by an average of 4.9 and 9.3d for the LQ and IG functions respectively compared with higher parity cows. Lactation persistency was significantly ($P < 0.05$) and comparatively higher in first parity cows than older cows. Average milk yield fitted as a covariate but not shown in Table 8.1 significantly ($P < 0.001$) influenced lactation parameters and therefore curve shapes.

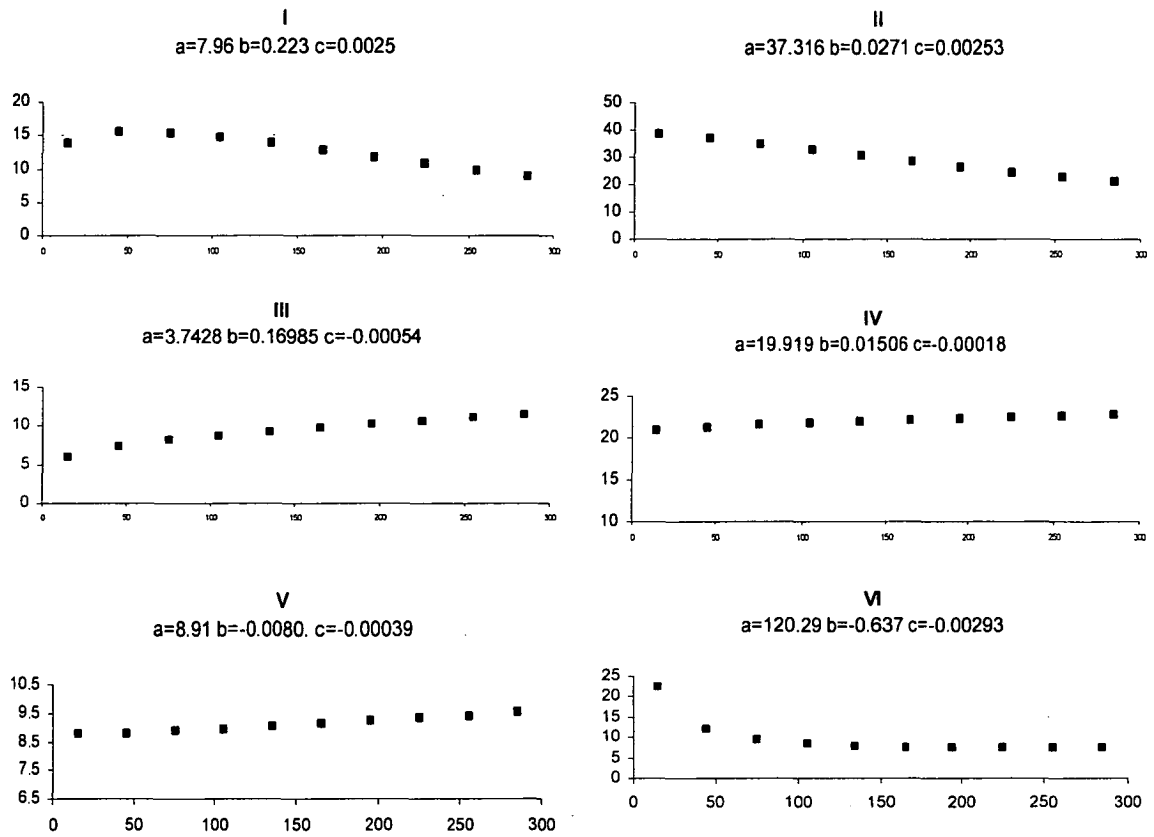


Figure 8.1. Different curve shapes detected by fitting 6908 individual lactation to the incomplete gamma function.

The incomplete gamma model is $y_t = at^b \exp^{-ct}$.

Curves types are I and II= Standard, III and V=continuously increasing, VI=Decline followed by incline and VII and VIII=continuously declining.

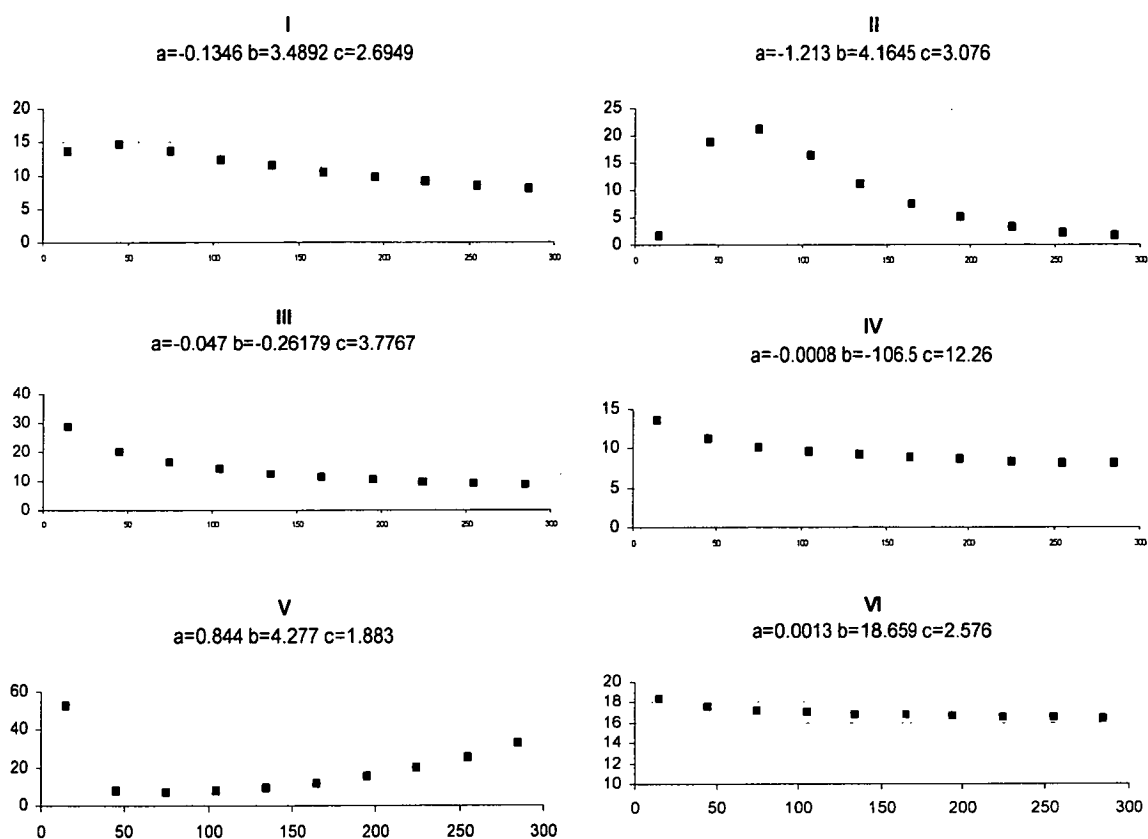


Figure 8.2. Different curve shapes detected by fitting 6908 individual lactation to the Log quadratic function.

The Log quadratic model is $\text{Log} y_t = a(b - \text{Log} t)^2 + c$

Curves types are I and II= Standard, III and I=continuously declining V and VI = Decline followed by incline and VII and VIII continuously increasing.

Environmental factors:

The main environmental factors affecting the shape of lactation curves were year and season of calving (Table 8.3). All the parameters of the LQ function were significantly higher ($P < 0.01$) in cows that calved in 2006 compared to cows calving in other years. Similarly, the initial milk yield (IG function) was significantly higher ($P < 0.01$) in FF cows calving in 2006 but the rate of incline to peak was higher in cows that calved in 2007. The decline rate (parameter c of the IG function) did not differ between calving years. Cows calving in the autumn and summer seasons had significantly ($P < 0.01$) higher rates of incline (parameter a) to peak milk yield (LQ model), whereas winter calving cows attained higher rate of incline (parameter b) to peak milk yield (IG model), than cows calving in other seasons

In the LQ function, cows calving in 2007 attained peak milk yield three days later than those calving in the other years (Table 8.3.). Peak milk yield did not differ between calving years (LQ function) but cows calving in 2006 attained significantly ($P < 0.01$) higher peak milk yield than those calving in the other years (IG model). Spring and winter calving cows attained significantly ($P < 0.05$) higher peak milk yield and attained peak yield at a later date than cows calving in the other seasons. Similarly, irrespective of model type, cows calving in autumn and winter were more persistent in post-peak milk yield than cows calving in other seasons.

The interaction of calving year and calving season influenced the lactation parameter estimates of both functions (Table 8.4). Irrespective of calving year, cows calving in the summer had the highest rate of incline to peak milk yield, parameter a of the LQ function, whereas the parameter b which refers to similar lactation curve trait was highest in winter-calving cows in the IG function. Winter and spring calving cows produced the highest amount of milk at peak (LQ) irrespective of calving year compared with cows calving at other seasons. Peak milk yield did not differ significantly between cows calving in both seasons. Similarly, autumn calving cows attained peak yield at a later day than cows calving at other seasons irrespective of calving year. In the IG function, although initial milk yield did not differ between cows calving in the different seasons in 2005, FF cows calving in the summer and spring seasons produced significantly ($P < 0.01$) more milk at lactation initiation than cows

calving in the other seasons. Similarly the rate of incline to peak (parameter b) did not differ between cows calving in the different seasons in 2006 but winter-calving cows had significantly higher rate of incline to peak than cows calving in the other seasons. Finally the decline rate was higher in spring and winter calving cows except in 2005 when decline rate did not differ among cows irrespective of season of calving.

8.4.3 Genetic attributes of lactation parameters

The genetic attributes of the lactation parameters are shown in Tables 8.5 and 8.6. The heritability (h^2) of parameter a and c were higher than the of parameter b (IG function). Of the three parameters of the LQ function, the h^2 of the parameter measuring peak yield was highest, being 0.14 compared with 0.05 for the rate of incline to peak yield. The h^2 of day at peak was the lowest in the LQ function whereas the h^2 of the rate of incline was the lowest in the IG function. Apart from the heritability of parameter a and peak yield which was higher in the IG function, the other parameters of the lactation curve traits were higher in the LQ model. Phenotypic correlations among parameter estimates of the IG model ranged from -0.81 to 0.83, and -0.59 to 0.92 in the LQ model. The strongest phenotypic correlations were between parameters a , b , c , persistency and peak day yield as well as between parameter b and persistency (IG model). The strongest phenotypic correlations among the parameters of the LQ model were between parameters b and day at peak and between parameter c and peak milk yield. The phenotypic correlations among parameters a , b , persistency and peak day were strongly negatively correlated, while those among persistency, parameter b and *peak day* were positive (IG model). The phenotypic correlations among all the lactation parameters of the LQ model were negatively correlated with parameter a , but the correlations among the parameters b vs. peak yield, and c vs. peak yield and persistency were positive.

Genetic correlations of the IG model parameters were highest among parameters a , b , peak day and lactation persistency and between persistency and peak day. High genetic correlations among parameters of the LQ model were found between parameters a , and c vs. persistency and peak yield and among parameters b vs. c , and peak day. Nearly all the phenotypic correlations were significant among the parameters of both models; genetic correlations on the hand, were only significant between parameters a , peak day and persistency (IG model). There were significant genetic correlations among the LQ

and persistency (IG model). There were significant genetic correlations among the LQ model parameters c , persistency and peak milk yield as well as between parameter b and day at peak.

Table 8.5. Additive and residual variances and heritability (\pm se) of lactation parameter estimates obtained from multivariate analysis of 5597 (IG) and 6907 (LQ) individual cows lactations.

Model	IG			LQ		
Parameter	Additive variance	Residual variance	Heritability	Additive variance	Residual variance	Heritability
a	1.37	18.98	0.07(0.001)	0.0008	0.015	0.05(0.022)
b	0.0016	0.04	0.04(0.0007)	0.018	0.44	0.04(0.020)
c	$0.39e^{-6}$	$0.55e^{-5}$	0.07(0.001)	0.0024	0.015	0.14(0.035)
Persistency	2.18	32.00	0.04(0.010)	4.39	25.56	0.15(0.059)
Peak yield	3.79	22.30	0.15(0.080)	3.64	28.80	0.11(0.46)
Peak day	2.35	30.26	0.07(0.031)	2.63	34.76	0.07(0.029)

Table 8.6. Phenotypic and genetic correlations (\pm se) among lactation parameter estimates of the IG and LQ functions obtained from bivariate analysis of individual cow's lactation data.

Model	Trait	a	b	c	persistency	Peak yield	Peak day
IG	a		-0.81 (0.005)	0.83 (0.004)	-0.77 (0.006)	0.20 (0.013)	-0.76 (0.006)
	b	-0.78 (0.222)		-0.56 (0.010)	0.81 (0.005)	0.12 (0.014)	0.60 (0.009)
	c	0.60 (0.402)	0.67 (0.218)		0.38 (0.012)	0.46 (0.104)	0.22 (0.303)
	Persistency	-0.99 (0.000)	0.26 (0.410)	-0.59 (0.301)		-0.28 (0.013)	0.83 (0.000)
	Peak yield	0.48 (0.288)	0.35 (0.387)	0.90 (0.104)	-0.76 (0.144)		-0.34 (0.012)
	Peak day	-0.83 (0.178)	0.39 (0.415)	-0.67 (0.303)	0.99 (0.000)	-0.78 (0.142)	
LQ	a		-0.51 (0.009)	-0.49 (0.009)	-0.59 (0.008)	-0.17 (0.012)	-0.53 (0.009)
	b	-0.13 (0.36)		-0.14 (0.012)	0.04 (0.013)	-0.49 (0.006)	0.86 (0.003)
	c	-0.49 (0.202)	-0.60 (0.218)		0.60 (0.008)	0.92 (0.002)	-0.44 (0.010)
	Persistency	-0.81 (0.121)	-0.54 (0.219)	0.76 (0.008)		0.68 (0.007)	-0.11 (0.012)
	Peak yield	-0.67 (0.210)	-0.59 (0.194)	0.85 (0.042)	0.94 (0.039)		-0.43 (0.010)
	Peak day	-0.009 (0.3220)	0.95 (0.000)	-0.43 (0.181)	-0.48 (0.182)	-0.60 (0.163)	

NB: Phenotypic (upper diagonal) and genetic (lower diagonal) correlations

8.5 Discussion

Since the shape of the lactation curve can be affected by genetic and non-genetic factors, a robust model should adequately mimic the biological process of lactation and adjust for factors affecting it. The two functions compared were the Incomplete Gamma (Wood 1967), and the newly proposed three-parameter Log Quadratic model. No direct comparisons of model parameters were made because the parameters of different lactation functions connote different biological events in the course of a cow's lactation. For instance, parameter a is a scaling factor which represent initial milk yield in the IG model whereas it is the rate of incline to peak or decline to nadir in the LQ function. Parameters b and c (IG) represent the incline and decline parts of the curve respectively, while these parameters represent the day at and value of peak milk yield respectively.

8.5.1 Variation in curves shapes

The two functions evaluated in this chapter adequately represented the various types of curve shapes that had been reported in previous studies (Olori *et al.* (1999), Tekerli *et al.* 2000 and Macciotta *et al.* 2005). However, the plots of the IG model parameters showed that the size and magnitude of all the model parameters can potentially influence the shapes of the lactation curves. For instance, curves I and II (Figure 8.1) all had positive parameters but the difference of 28.8 and -0.233 in the values of parameter a and b resulted in a continuously declining shape (II) compared with the standard or typical shape (I). Similar differences were noted in the curves V vs. VI. Previous studies had indicated that parameters b and c of the IG model determined the shape of the curve (Wood 1967, Olori *et al.* 1999). A random evaluation of the model goodness of fit of the individual cows whose predicted values were used for the plots did not show great differences in the goodness of fit except curves V and VI (Figure 8.1) whose mean square error values were 104.32 and 44.709 respectively. It can therefore be assumed that the sign of the parameter *per se* may not be the sole determinant of differences in curve shapes.

The occurrence of *atypical* curve types in nearly 35% of the individual cow data fitted to the IG model confirmed previously reported frequency of occurrence of these curve types in dairy cows (Macciotta *et al.* 2005, Olori *et al.* 1999, Rekik and Ben Gara, 2004). These differences are attributable to the genetic make up and genotype x environment

interaction effects resulting in different expressions of production merits in dairy cows. However, the lower percentage of the number of cows exhibiting the *atypical* curve types when the same data were fitted to the LQ model seems to suggest that the mathematical property of the function can potentially influence the frequency of non-standard curve types. Similar conclusions were made in the study of Landete-Castillejos and Gallego (2000) in which the data fitted to the modified gamma model (Jenkins and Ferrel 1984) always returned a standard curve type whereas other models described more curve shapes.

8.5.2 Factors affecting lactation curve

Physiological factors

The effect of factors affecting the lactation curve shapes were compared among only the *typical* curve types as Macciotta *et al.* (2005) had suggested that comparisons among parameter values and (co)variances, could yield more robust, reliable, and easily interpretable results if performed within groups based on curve shape. The lower initial and peak milk yields in first-parity compared to later-parity cows observed in this study are in agreement with the reported effect of parity on test-day milk yield (Tekerli *et al.* 2000). Other reports (Rowlands *et al.* 1982) showed that second-parity cows attained earlier peak yields than first-parity cows. Hansen *et al.* (2006) reported breed and parity effects on curve parameters. In a typical lactating cow, milk production increases with age and parity due to increased body weight, larger capacity for dry matter intake, increased udder size and recurrence of pregnancy and lactations (Capuco *et al.* 2001). Higher lactation persistency in first-parity cows compared to older cows, as demonstrated in this study, are consistent with reported studies on lactation persistency (Pérochon *et al.* 1996). Higher lactation persistency in primiparous cows is attributed to the preferential partitioning of nutritional energy towards maturity and mammary gland development rather than to increase milk yield in animals that are still growing.

Season and year of calving

Year and season of calving affected the shape of the lactation curves in both models. Differences in curve shapes due to season and year of calving have been reported (Macciotta *et al.* 2006, Tekerli *et al.* 2000). Wood (1970) noted that parity and season of calving were the dominant factors with the greatest influence on the lactation curve and

suggested the inclusion of these two factors in a model for a more accurate prediction. Under pasture-based systems, annual variation in rainfall and temperature at critical lactation stages can affect milk yield. For instance, a reduction in quantity and quality of pasture in the summer months due to reduced rainfall and high temperatures in the Southern Hemisphere depresses milk yield. Similarly, cows calving in spring and winter produce more milk in early lactation than cows calving in autumn and summer because of the coinciding of peak milk yield with period of lush pasture (Lennox *et al.* 1992).

Seasonal influence on lactation is thought to be mediated by the interaction of day light and ambient temperature (Whittemore 1980). Heat stress is especially harmful to peak milk production. There is significant environmental influence on the expression of heritable traits in dairy cows and production per cow varies between locations even under similar management practices (Garcia and Fulkerson 2005). Herd location (Batra 1986), region and herd practices, day of the year (including weather conditions), month of calving, days in milk and medical treatments have been reported to have significant effects on test-day yields for Holstein-Friesian dairy cows (Jamrozik and Schaeffer 1997, Val Arreola *et al.* 2004). The unequal data size, especially the relatively small data size of cows autumn-calving cows is also partly implicated in the result of this study. Similarly, the pooling of parities greater than 2 as parity 3 will tend to inflate the error bias of the results.

Studies on the influence of environmental factors on the occurrence of *atypical* curve types, (Macciotta *et al.* 2006 and Rekik and Ben Gara 2004), associated lateness in MID with differences in curve shapes. This study confirmed that not only *atypical* but also *typical* lactation curve shapes can vary due to differences in time of first test-day. Pollott and Gootwine (2000) had reported that poor goodness of fit in some lactation models are due to limitation in available records during this phase. The interaction of calving year and season observed in the study is attributed to variation in climate pattern between the production years pasture-based dairy cows are especially responsive to short-term variation in climatic conditions than cows managed under stall feeding or intensive systems (Tozer and Huffaker 1999, Rekik and Ben Gara 2004). This observation suggests the need to pay special attention to the nutrition of pasture-based dairy cows.

8.5.4 Genetic attributes of the model parameters

As mentioned previously incomplete data and missing pedigree information on some cows affected the precision of estimating genetic parameters. The results of the heritability should therefore be interpreted in the light of the limitations imposed by data quality. The heritability of parameter estimates of the IG model observed in this study was lower than values reported for the same parameters (Ali and Schaeffer 1997, Rekaya *et al.* 2000). However, the phenotypic and genetic correlations for the same pair of traits in both models are similar to values reported by Rekaya *et al.* (2000), except the phenotypic correlation between parameters a and c (IG model) and the genetic correlation between parameters a and c (LQ model) which were smaller. High genetic correlation between parameter a and b of the IG model, found in this study are also consistent with the reported finding of the authors. The differences may be attributed to the relatively small sample size and the properties of the data used in this study compared with the number of individual cows used in referenced studies. It is also possible that the restriction of the data used in this study to only *typical* lactations might have reduced the variation between individual cows thus lowering heritability. High phenotypic and genetic correlations between parameters b and c of the LQ model are not unexpected because these parameters are essentially the same.

8.6 Conclusion

This chapter determined the factors affecting lactation curve shapes of pasture-based Holstein Friesian cows and the genetic attributes of parameter estimates of the IG and LQ models. The parameters of both models were significantly affected by physiological and environmental factors although the extent of influence varied slightly between parameters estimates. Some of the differences in the observed effects of environmental and management factors on the shape of lactation curves may be an artefact of the mathematical properties of both models and should be borne in mind when using these models. The limitation imposed by the data size, the restriction of data to only typical lactations and the incomplete pedigree records possibly affected the heritability estimates. However, phenotypic and genetic correlations were however consistent with reported values and suggests that the parameters of the models can be used to genetically influence the lactation profile.

The study confirmed the relevance of environmental factors on lactation curve parameters and shape which should be borne in mind when assessing the goodness of fit of lactation curves. The influence of calving year and season on curve attributes is a pointer the need for coping strategies to deal with short- or long-term environmental factors which can potentially affect feed quality and by extension daily milk yield in pasture-based cows. Great variation in herd performance across dairy regions in Tasmania suggests the potential for individual cow milk yield improvement through the adoption of proven management practices that are suitable for the different dairy regions of Tasmania.

Chapter 9. Modelling the lactation of pasture-based dairy cows grazing at varying stocking rates and grain supplementation levels

9.1 Summary

In the last chapter, repeated measures regression model was used to evaluate the factors affecting the shape of lactation curves and to estimate the genetic attributes of lactation parameters. In this chapter of the thesis, the objective was to utilise a suitable function to simultaneously account for herd based non-genetic factors affecting the shapes of lactation curves. In view of the limitation of parametric empirical functions and the differences in data size for the different traits in the available data, the semi-parametric model, cubic splines was used, in ASReml platform, to fit experimental data on milk, protein and fat yields of mixed parity, pasture-based Holstein-Friesian cows. In this chapter, use of production level in early lactation as predictor of 305d milk yield with lactation curve was also tested. Furthermore, the effects of stocking rate (SR) and supplementation on milk yield and composition were investigated. Cubic splines were fitted to bi-weekly milk and milk composition data from four experimental treatment groups (low SR without grain, low SR with grain, high SR without grain and high SR with grain) over a 3-year period in which a total of 112 cows were randomly allocated to stocking rates of 2.3 or 3.4 cows/ha and 0 or 500kg of grain supplementation/cow/lactation. Lactation data were subjected to stepwise regressions, mixed model and restricted maximum likelihood analyses in SAS and ASReml utilising an animal model with cow and splines of days in milk (DIM) fitted as random effects. Age at calving was used as a covariate, while treatment, calving year, season, parity, days in lactation and their interactions were treated as fixed effects. Grain supplementation increased initial, peak and nadir milk yields and lactation length in the low SR treatment. Total milk, protein and fat yields per cow per hectare, feed efficiency, liveweight gains, calving interval and number of days to conception were higher in high SR treatments. The study demonstrated the application of cubic splines in modelling fat, protein and lactation profiles of pasture-based dairy systems, greater flexibility at the cost of additional computation and capability of picking up features of the lactation curve that are missed by traditional empirical and mechanistic models.

9.2 Introduction

The main aim of modeling lactation in dairy cows is to predict, with minimum error, the average daily milk yield after adjusting for various environmental factors. Santos and Silvestre (2008) reported that establishing lactation curves facilitates the estimation of milk yield and variation of milk constituents at different stages of the lactation and provides important information relative to weaning time and supplementation. Therefore, an accurate knowledge of the lactation curve is essential for breeding, economic and management decisions (Schaeffer 2004, Jensen 2001, and Swalve 2000), early detection of metabolic diseases like mastitis and sub clinical ruminal acidosis, and forecasting herd or individual cow performance (Schaeffer 2004). In modelling the milk, fat and protein yields of Holstein cows, Dematawewa *et al.* (2007) compared 9 empirical and mechanistic models and reported considerable computational problems associated with large mechanistic models and the relative predictive ability of the other models. In addition to biological (Pollot, 2004), empirical and mechanistic models (Swalve 2000), the application of Legendre polynomials (Kirkpatrick *et al.* 1994) and splines (White *et al.* 1999; Macciotta *et al.* 2005; Silvestre *et al.* 2006) to model lactation in dairy cows appears to be gaining popularity. Bohmanova *et al.* (2008) compared Legendre polynomials with 3 alternative models fitting linear splines to production traits in Canadian Holstein cows. They reported that models with splines gave lower estimates of variances at extremes of lactations, smaller prediction errors and higher stability of estimated breeding values than the model with Legendre polynomials. Although differences among models in goodness of fit measured by percentages of squared bias, correlations between predicted and observed records, and residual variances were small, the deviance information criterion favoured the spline model with 6 knots compared with the model with Legendre polynomials.

Cows do vary in their rate of daily milk yield and also rate of growth (particularly in the younger cows). These variations both lead to heterogeneity of variance over time. Furthermore, within treatment combinations, there are possible changes in milk, fat and protein yields with time. These lead to non-stationarity or complex patterns in the covariance structure that are typically very difficult to model parametrically because a simple transformation neither mitigates nor alleviates this difficulty (Verbyla *et al.* 1999). This is where cubic splines come in handy not only to smoothen the trends, but

also to deal with statistical dependence and variance heterogeneity, especially when used in conjunction with random coefficients in a mixed model framework to provide greater flexibility. Other advantages and uses of cubic splines have been extensively covered by Speed (1991) as a best linear unbiased predictor; Wahba (1985); Kimeldorf & Wahba (1970).

A cubic spline is a smooth curve over an interval formed by linked segments of cubic polynomials at certain knot-points, so that the whole curve and its first and second differentials are continuous over the interval (Green and Silverman, 1994). Verbyla *et al.* (1999) demonstrated that cubic splines are particularly convenient because they can be incorporated into a suitably constructed mixed-model framework. The ASReml software (Gilmour *et al.* 2006) has made the computations practical thus enabling White *et al.* (1999) and Silvestre *et al.* (2005) to apply this methodology to estimate genetic parameters for dairy cow lactation curves. More recently, Silvestre *et al.* (2006) and Bohmanova *et al.* (2008) compared many models including random regression models with Legendre polynomials and linear splines and demonstrated that models with splines had the best overall performance based upon goodness of fit measured by the lowest percentages of squared bias, highest correlations between predicted and observed records and lowest residual variances. Only few published studies in pasture-based dairy systems (Horan *et al.* 2005; MacDonald *et al.* 2008) have investigated the effect of stocking rates on the shape of the lactation curve over the entire lactation period and none utilized cubic splines. Silvestre *et al.* (2005) stated that no information is available on the use of splines for modelling fat and protein yields in dairy cattle, hence the need for this study. Therefore, our objectives were to utilize and ascertain the accuracy of prediction of cubic splines in modelling protein, fat and lactation profiles and to investigate the effects of stocking rate and grain supplementation in pasture-based dairy cows.

9.3 Materials and methods

9.3.1 Experimental design, animals and management

This study was carried out at the Elliott Research and Demonstration Station in North-Western Tasmania, Australia, located at latitude 41° South, longitude 146.8° East. The experiment had a University of Tasmania Animal Ethics Approval Permit No.

A0009110 and was conducted in accordance with the 1993 Tasmanian Animal Welfare Act and the 2004 Australian Code of Practice for the Care and Use of Animals for Scientific Purposes. The experiment was a 2x2 factorial trial comprising two stocking rates (SR) of 2.3 and 3.4 cows/ha (being low and high SR treatments, respectively) and two grain supplementation levels, 0 and 500kg crushed barley/cow/lactation being no-grain and grain supplemented treatments. The treatment groups were: 1. Low SR no grain (LN), 2. Low SR with grain (LG), 3. High SR no grain (HN) and 4. High SR with grain (HG). A total of 112 Holstein-Friesian cows of mixed parity were randomly assigned to the treatment groups and monitored over three production years (1994/95 – 1996/97). Each treatment group was reared as a herd. Grain was generally introduced to maintain intakes during periods of reduced pasture availability in early spring, summer and autumn corresponding to the months September to November, December to February and March to May, respectively. No other buffers or additives were included in the diets. Annual rainfall at the study site ranged from 1047mm in 1994 to 1547mm in 1996. Maximum temperature was 15.0, 14.7 and 14.5⁰C, respectively for years 1994, 1995 and 1996, while minimum temperature for the same period averaged 6.4⁰C. Mean annual evaporation, radiation and vapour pressure were 2.7 mm, 14.7MJ/m² and 10.4 hPa respectively, while relative humidity percentages at maximum and minimum temperatures were 97.1 and 61.4, respectively.

Herd reproductive management was aimed at producing a 6 to 8-week condensed calving pattern, with 50% of the cows calving within 18 days or less. Synchronization programs were not used in either milking cows or heifers, although non-cycling cows were treated with cattle insert progesterone (CIDR) and/or prostaglandin injections. Cows were artificially inseminated over a 5-6 week mating period, after which bulls were used for the remainder of the mating period. The structure of the four treatments and management parameters are shown in Table 9.1.

9.3.2 Data editing

Although the study lasted three years data on the analysis of fat and protein were available only for the third year. Therefore two data sets were utilised for modelling the lactation curves. The first data (DATA1) consisted of 10,310 weekly milk yield records on 484 lactations while DATA2 consisted of 1,414 test-day records of milk, fat and

protein on 160 lactations of the approximately 112 Holstein-Friesian dairy cows. involved in the stocking rate and grain supplementation trial. All data sets were edited to exclude cows with unknown birth and or calving dates or with lactation length less than 100 days. Records of milk, fat or protein yields recorded before 4 days post-partum and after 306d were also excluded. Lactation length was grouped as 1=short ($100 < LL \leq 50$), 2=medium ($150 < LL \leq 250$) and 3=normal ($LL > 250$), days. Parities (P) > 2 were pooled. In order to test the hypothesis of no effect of early lactation production level (PL) on the lactation profile, three production level classes based on average daily milk yield during the first 5-85 days in milk, adjusted for parity and production year were defined for DATA1 and DATA2. These are average daily milk (M) yield $< 17\text{L/d}$, $17 < M \leq 25\text{L/d}$ and $M > 25\text{L/d}$ being low, medium and high production levels respectively. Additional data collected throughout the three seasons were lactation length (LL), calving interval (CI) and days to conception (DC), weekly records of pre and post-grazing pasture mass and pasture growth rates, monthly liveweights, body condition score and liveweight gains.

Table 9.1. Structure of the treatment group.

Treatment group:	LN ¹	LG	HN	HG
Stocking rate (cows/ha)	2.4	2.4	3.4	3.4
Farmlet area (ha)	13.2	13.3	7.1	7.1
Number of paddocks	20	20	18	17
Herd size	32	32	24	24
Calving start date	Aug 1st	Aug 1st	Aug 1st	Aug 1st
Irrigation	0	0	100	100
Grain fed (kg/cow/year)	0	500	0	500
Fertiliser				
kg elemental nitrogen/ha	100	100	100	100
kg elemental phosphorus/ha	60	60	60	60
Potassium	60 kg elemental potassium/ha applied where soil levels were below 300 ppm			
Silage and hay	Conserved from genuine surplus only. No purchased silage or hay fed during lactation			
Off-farm grazing (agistment)	Dry cows and all replacements			

¹Treatment = LN (Low SR No Grain), LG (Low SR Grain), HN (High SR No Grain) and HG (High SR Grain)

9.3.4 Statistical analyses

The lactation curve data were analyzed using restricted maximum likelihood procedures with an animal model in ASReml (Gilmour 2006), with day in milk (DIM), treatment (T), test year (TY), P, calving season (CS) and PL and their significant interactions as fixed effects while cow and the splines of cows were random effects. Splines curve were obtained for the fixed effect classes (T, TY, P, CS and PL). Only significant interactions were included in the final model. In the analysis of milk yield (DATA1) and milk constituents (DATA2) stepwise regressions of all explanatory variables and their interactions were tested before arriving at a parsimonious model. Age at calving was included as a covariate in the earlier models but dropped in the final model as it was not significant.

9.3.5 Model evaluation for goodness of fit

The following criteria were used to evaluate the fitness of the model: Correlation between actual and predicted milk yield, average and standard deviation of errors for the treatments, which measure the error in absolute terms without recognizing its variation through the lactation (Guo and Swalve, 1995) and Durbin Watson statistic (D) for presence of autocorrelation between records. The statistics is given

$$\text{as } D = \frac{\sum_{i=2}^n (e_i - e_{i-1})^2}{\sum_{i=1}^n (e_i)^2}$$

The Durbin-Watson statistic (D) tests for the presence of first order autocorrelation in the error by comparing the significance of the correlations between the errors of **DIM** *t* with the error from **DIM** *t-1* (Seber and Wild, 1989). The Durbin-Watson statistic has a range from 0 to 4; D values near 2 indicate absence of correlation. Values of D near zero indicate positive autocorrelations i.e. closeness of successive errors, while values near 4 are indicative of negative autocorrelation (Durbin and Watson, 1951).

d) Percentage of estimated milk yields <0 or > 35 (Silvestre *et al.* 2006). Mean daily milk yield of the 10,309 records was 18.97, of which only 47 had milk yield >35L corresponding to an expectation of 0.34. The model was considered inadequate if the

proportion of predicted milk yield values >35 differed significantly from the expectation or any of the predicted values were <0 which is biologically impossible.

9.4 RESULTS

9.4.1 Lactation curves: Influence of treatment

The lactation profiles of the Holstein-Friesian cows depicting the relationship between milk yield and pasture growth rate in the different treatment groups and lactation stages/days in milk (DIM) are depicted in Figure 9.1, while the mean daily milk, protein and fat yields as influenced by treatment (T), parity (P), calving season (CS), test year (TY) and production level (PL) are portrayed in Table 9.2. It was clearly evident from Figure 9.1 that the grain-supplemented group of cows on high (HG) and low (LG) stocking rates (HG) had the highest milk yield, peaks and persistency, while the non-supplemented cows on both high (HN) and low (LN) stocking rates had the least values but the fastest decline phase up to 270 DIM. These treatment differences were highly significant ($P<0.001$) and varied with DIM as the cows advanced in their lactation stages. Figure 9.1 also shows that cows on the low SR treatments exhibited the typical lactation curve patterns i.e. a rise to peak, followed by decline to nadir. Cows on the HN treatment attained peak yield at first DIM and maintained production level for about 50-60 days postpartum before declining to nadir level at 271 DIM. Cows in the HG treatment on the other hand, showed the typical curve shape with a rise to peak but also attained a second peak at 125-150 DIM before gradually declining to nadir at 305 DIM. The difference in daily milk yield between the LN and LG treatments in early lactation up to peak DIM was <0.50 L. However, from about 120 DIM when supplementation commenced, this difference increased to between 2.0 – 3.4 L/d and was sustained until about 270d postpartum. Similar trends were observed between the supplemented and non-supplemented high SR treatments. The highly significant variations ($P<0.01$) in milk, fat and protein yields attributable to P, TY and PL are obvious in Table 9.2 depicting that third-parity cows calving during the spring season produced more milk and component yields than first-parity and winter calvers with those of them in the high production levels (PL) clearly surpassing their counterparts in the low and medium PL (Figure 9.2).

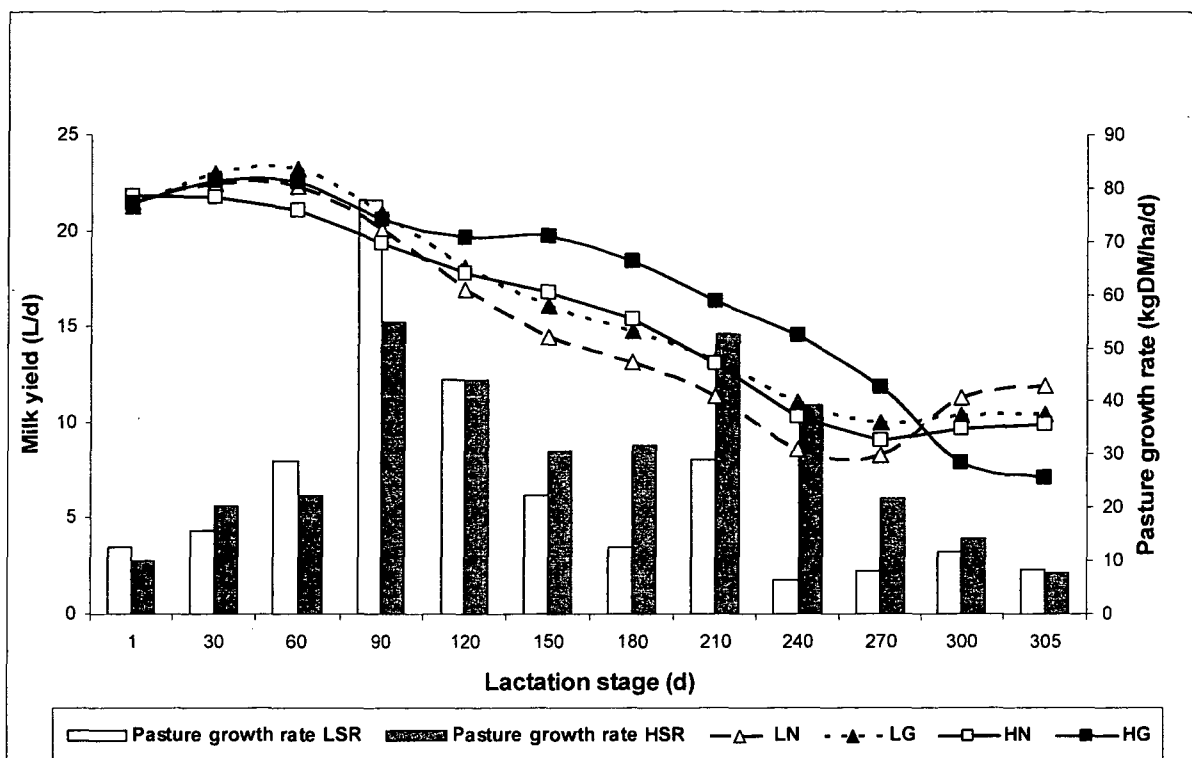


Figure 9.1. Effect of treatment on lactation profile of Holstein-Friesian dairy cows and low and high stocking rate effect on pasture growth rate

*NB: Lactation stage DIM 1, 30 corresponds to the months of July, 31-60 =August ...etc

*Treatment = LN (Low SR No Grain), LG (Low SR Grain), HN (High SR No Grain) and HG(High SR Grain)

The outcome of fitting cubic splines to the lactation profile and subsequent predictions of initial, peak and nadir milk yields in different treatment, parity, year, season and production groups are presented in Table 9.3. It shows that initial milk yield did not differ between the HG and HN treatments, but both were higher ($P < 0.05$) than the yield for the LG and LN treatments (Table 9.3 and Figure 9.1).

9.4.2 Season of calving, parity and production level

Mean initial daily milk yield was lower ($P < 0.05$) for spring calving cows than for winter calving cows (Table 9.3). Daily milk yield peaked at 46 DIM, declined more rapidly to nadir at 9.45L at 274 DIM. In winter-calving cows, daily milk yield peaked at 1 DIM and remained high for up to fifty days postpartum before declining intermittently to reach nadir at 293 DIM. Consequently, winter calving cows showed greater persistency and had higher total milk yield than spring calving cows.

Table 9.2. Influence of treatment, parity, calving season, test year and production level (Mean \pm se) on daily milk, fat and protein yields of dairy cows (number of observations in parentheses)

Item	Milk (L)	Fat (g)	Protein (g)
<i>Treatment*</i>			
LN	18.8 \pm 0.12 (2,529)	372.7 \pm 8.68 (226)	288.8 \pm 7.27 (226)
LG	18.9 \pm 0.11 (3,025)	415.7 \pm 7.76 (308)	331.1 \pm 6.95 (308)
HN	18.4 \pm 0.12 (2,402)	364.3 \pm 9.64 (215)	283.8 \pm 8.61 (215)
HG	19.8 \pm 0.11(2,353)	383.3 \pm 8.31 (206)	305.4 \pm 8.31 (206)
<i>Parity[§]</i>			
1	16.3 \pm 0.09 (2,488)	313.4 \pm 6.19 (257)	243.9 \pm 5.51 (257)
2	18.4 \pm 0.13 (1,708)	373.4 \pm 8.31 (198)	299.8 \pm 7.68 (198)
3	20.2 \pm 0.08 (6,113)	430.1 \pm 6.18 (500)	338.3 \pm 5.71 (500)
<i>Calving Season[†]</i>			
Spring	20.5 \pm 0.14 (2,017)	416.5 \pm 15.20 (859)	334.2 \pm 4.02 (859)
Winter	18.6 \pm 0.00 (8,292)	383.6 \pm 4.49 (96)	301.6 \pm 14.52 (96)
<i>Test Year[‡]</i>			
1994/95	20.2 \pm 0.11 (3,129)	na	na
1995/96	18.9 \pm 0.09 (3,515)	na	na
1996/97	18.1 \pm 0.09 (3,665)	387.9 \pm 3.96 (955)	277.7 \pm 3.52 (955)
<i>Production level[#]</i>			
Low	13.9 \pm 0.10 (974)	na	na
Medium	18.2 \pm 0.10 (6,243)	na	na
High	22.2 \pm 0.11 (3,092)	na	na

*Treatment = LN (Low SR No Grain), LG (Low SR Grain), HN (High SR No Grain) and HG (High SR Grain)

[§]Parity = (Parities >2 were pooled and labelled Parity 3)

[†]Calving Season, Spring = September–November, Winter = June–August

[‡]Test year = Daily fat and protein yields only available in 1996/97. na = not available

[#]Production Level, L=Low: PL \leq 17, medium: 17<PL \leq 25, high: PL>25

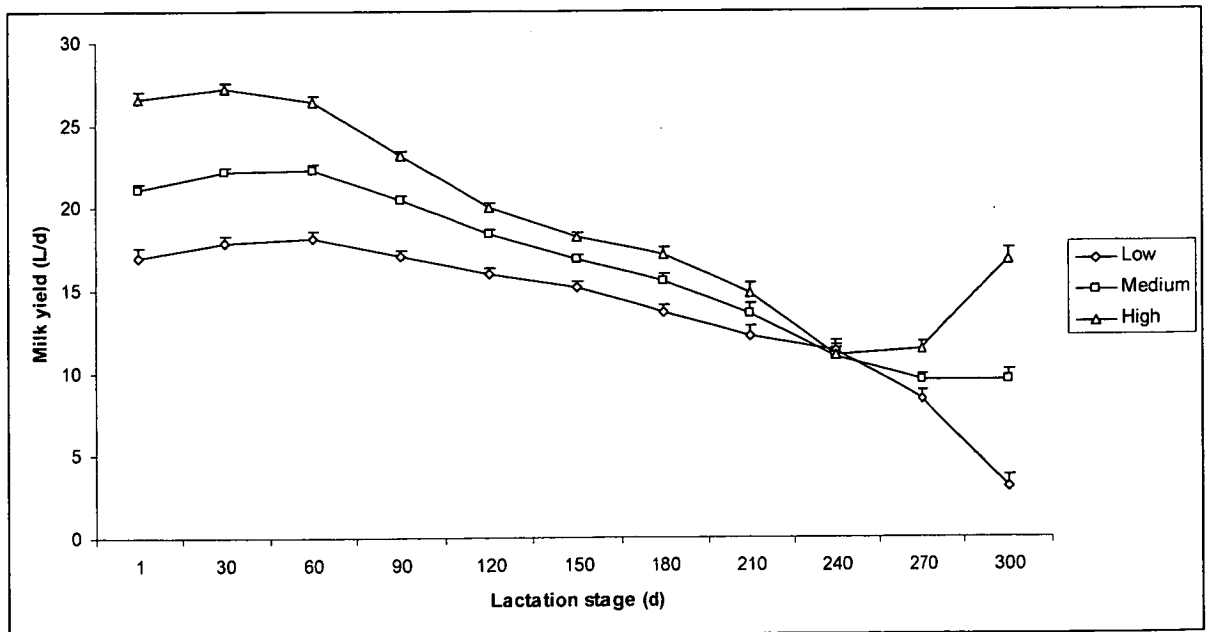


Figure 9.2. Effect of production level in early lactation on the lactation curve of Holstein-Friesian dairy cows

*Production level = mean milk yield (L/d) at DIM 5-85, Low: PL \leq 17,, medium: 17<PL \leq 25 and high: PL>25

Mean initial and peak daily milk yield were lower but more persistent, in first-parity compared with later parity cows. Production level significantly influenced initial and peak milk yields in a similar pattern as parity (Table 9.3 and Figure 9.2). Cows producing at high level in early lactation (DIM 4-85) attained significantly higher ($P<0.01$), initial, peak and total milk yield than cows producing at medium and low levels. High-producing cows yielded more milk per day from lactation initiation up to 200 days postpartum, and attained an earlier peak yield by an average of 14 days, compared with low producers, although the latter were more persistent in production.

9.4.3 Milk, fat and protein curves

Fat yield (g/cow/d) declined from first DIM to reach a temporary low level at 100 DIM, before declining to nadir level at the end of lactation (Figure 9.3). In all treatments, initial and peak fat yields occurred on first DIM and reached nadir at the end of lactation. Nadir fat yield was lowest for the HG treatment and highest for the LG treatment. Initial protein yield was lowest in the LN and highest in the LG treatment. Except for the LG group, cows in the other treatments attained double nadir protein yields at 50-120 DIM and towards the end of the lactation period, respectively. All the treatments attained a second peak protein yield at 220-250 DIM (Figure 9.3). Post-peak protein yield decline was steeper in the high SR than in the low SR treatments, although the former attained a second peak yield during mid-lactation and had higher ($P<0.05$) daily yields. Initial and mid-lactation MP yield were similar for the two high SR treatments until about 120 DIM when cows in the supplemented treatment produced 60-70g more protein than their unsupplemented counterparts. On the other hand, cows on the LG treatment maintained about 70-80g daily MP yield advantage over the LN treatment throughout lactation.

Table 9.3. Cubic spline model predicted values of daily initial, peak, nadir and total milk yields and corresponding day at peak and nadir of Holstein-Friesian cows as influenced by treatment, parity, test year, calving season and production level

Factor	Test-day milk yield (L/d)* parameters with standard errors					
	Initial	Peak	Day at Peak	Nadir	Day at nadir	Total†
Treatment (T)*						
LN	21.3 ^b	23.7 ^b	49	7.9 ^c	251	4,661 ^d
LG	21.2 ^c	23.5 ^c	49	9.9 ^a	273	5,034 ^b
HN	21.7 ^a	21.9 ^a	1	9.0 ^b	271	4,864 ^c
HG	21.7 ^a	21.9 ^a	45	7.2 ^d	305	5,464 ^a
SED‡	0.66	0.66		0.66		155
Parity (P)§						
1	20.4 ^c	21.3 ^c	41	8.4 ^c	305	4,604 ^c
2	21.5 ^b	22.5 ^b	42	9.7 ^b	280	4,974 ^b
3	22.4 ^a	24.1 ^a	47	10.8 ^a	276	5,428 ^a
SED	0.51	0.51		0.51		126
Test year (TY)						
1994	23.2 ^a	24.2 ^a	44	11.6 ^a	269	5,506 ^a
1995	20.8 ^b	22.6 ^b	47	8.1 ^b	263	4,770 ^b
1996	22.4 ^a	22.5 ^b	1	9.3 ^c	268	4,869 ^b
SED	0.94	0.94		0.94		211
Calving Season (CS)†						
Spring	20.7 ^b	23.2 ^a	46	9.5 ^b	274	4,935 ^b
Winter	22.1 ^a	22.5 ^b	1	9.8 ^a	293	5,069 ^a
SED	0.51	0.51		0.51		124
Production level (PL)#						
Low	16.9 ^c	18.3 ^c	50	2.1 ^c	305	4,214 ^c
Medium	20.9 ^b	22.5 ^b	47	9.4 ^b	283	4,994 ^b
High	26.5 ^a	27.3 ^a	36	10.4 ^a	254	5,799 ^a
SED	0.54	0.54		0.54		131

*Treatment = LN (Low SR No Grain), LG (Low SR Grain), HN (High SR No Grain) and HG (High SR Grain)

§Parity (Parities >2 were pooled and labelled Parity 3)

†Calving Season, Spring = September–November, Winter = June–August

Production Level, L/d. Low: PL≤17, medium: 17<PL≤25, high: PL>25

‡SED – Overall standard error of difference obtained from prediction statement except in total milk yield, which is mean of standard errors

Means with different superscripts within columns in subgroups are different (P<0.05)

9.4.4 Stocking rate

A separate analysis of DATA1 for the effect of SR (not shown on tables) indicated that irrespective of SR, milk and protein yields were highest in 1994 and lowest in 1995 but fat yield was highest in 1995. Least square means of milk and constituent yields were lowest in first parity cows being, 3947 ± 36 , 158.8 ± 4.21 and 121.7 ± 2.96 , and highest in third and later parity cows at 4968 ± 53 , 203.2 ± 3.60 and 158.1 ± 2.62 for milk, fat and protein yields respectively. Cows in the high SR produced 10.36 kg more fat per lactation than those in low SR treatment. None of the tested factors except parity influenced somatic cell count.

All the tested effects except the interaction of CY & SR and CY, CS & SR significantly affected CI which was longer by 7 days in high SR treatment (Table 9.4). Calving interval was shorter in the 1995 being 354 ± 4 d compared with 366 ± 3 and 367 ± 4 in 1994 and 1996 respectively. First parity cows had significantly longer ($p < 0.0001$) CI which was higher by 9.4d and 6.8d than in second and later parity cows respectively. Similarly CI was higher in winter calving cows being 370.13 ± 3.04 d compared with 351.58 ± 3.04 for spring calving cows. Similar results were obtained for day to conception.

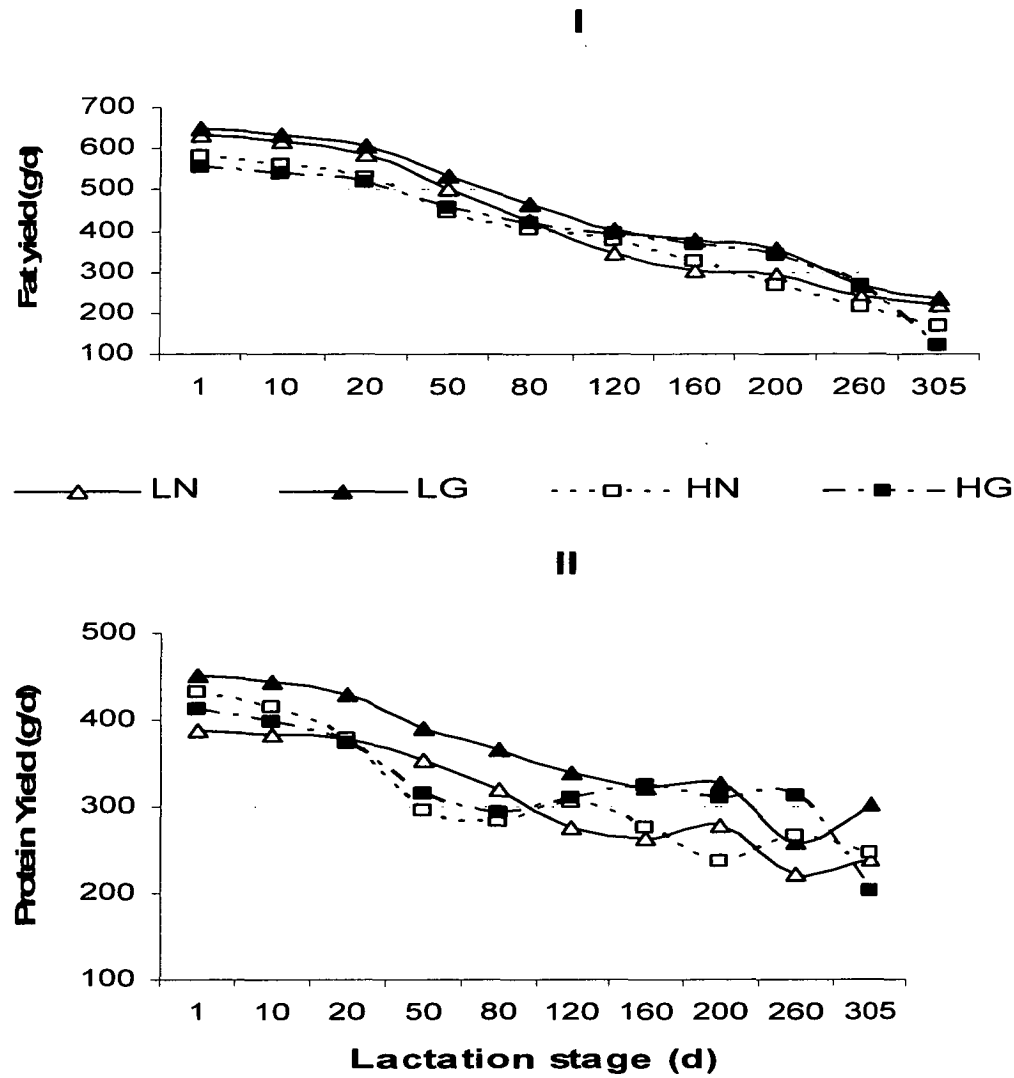


Figure 9.3. Effect of treatment on fat (I) and protein (II) yield profile of Holstein Friesian dairy cows.

Treatments are LN (Low stocking rate), LG (Low stocking rate + grain), HN (High stocking rate) and HG(Highs stocking rate +grain)

*Chapter 9. Modeling the lactation of pasture-based dairy cows grazing at varying
stoking rate and supplementation levels*

Table 9.4. Least square means (\pm se) of total milk, fat and protein yields, day to conception, lactation length and calving interval of cows in the experiment.

Factor	Traits/lactation					
	Milk (L)	Fat (kg)	Protein (kg)	Day to conception (d) (DC)	Lactation length (d) (LL)	Calving Interval (d) (CI)
Treatment (T) ^a						
LN	4290 \pm 100	170.9 \pm 3.91	135.2 \pm 2.77	94.3 \pm 3.16	232.2 \pm 2.56	364.9 \pm 2.88
LG	4779 \pm 127	188.3 \pm 4.79	151.4 \pm 3.53	89.6 \pm 4.22	258.1 \pm 2.82	359.6 \pm 4.22
HN	4348 \pm 129	179.3 \pm 5.13	136.5 \pm 2.58	91.4 \pm 4.28	261.5 \pm 2.77	361.4 \pm 4.28
HG	4759 \pm 146	186.8 \pm 4.57	150.8 \pm 4.05	93.9 \pm 4.62	266.0 \pm 2.99	363.9 \pm 4.62
Parity (P) ^b						
1	4201 \pm 117	159.9 \pm 4.26	129.0 \pm 3.26	96.2 \pm 4.21	253.9 \pm 2.97	366.2 \pm 4.21
2	4500 \pm 102	180.4 \pm 4.16	143.5 \pm 2.87	86.9 \pm 3.80	251.1 \pm 2.86	356.2 \pm 3.82
3	4930 \pm 93	203.8 \pm 3.56	157.9 \pm 2.59	94.3 \pm 3.16	258.3 \pm 1.79	364.3 \pm 3.16
P x T						
Parity1xLN	3962 \pm 169	155.7 \pm 6.53	123.4 \pm 4.71	na	232.5 \pm 4.89	na
Parity1xLG	4559 \pm 197	167.8 \pm 7.18	141.3 \pm 5.51	na	261.1 \pm 5.36	na
Parity1xHN	4063 \pm 190	157.9 \pm 7.32	121.5 \pm 5.33	na	264.9 \pm 5.26	na
Parity1xHG	4221 \pm 224	158.1 \pm 7.60	130.0 \pm 6.24	na	257.2 \pm 5.14	na
Parity2xLN	4301 \pm 161	171.1 \pm 6.55	135.8 \pm 4.53	81.1 \pm 5.38	224.9 \pm 5.12	351.1 \pm 5.38
Parity2xLG	4608 \pm 189	187.2 \pm 7.18	148.6 \pm 5.33	86.1 \pm 6.79	252.3 \pm 5.77	356.1 \pm 6.79
Parity2xHN	4508 \pm 185	181.7 \pm 8.23	143.3 \pm 5.20	85.5 \pm 6.54	257.3 \pm 5.56	355.5 \pm 6.55
Parity2xHG	4582 \pm 200	181.6 \pm 8.50	146.2 \pm 5.64	95.5 \pm 6.54	269.9 \pm 5.82	365.1 \pm 7.06
Parity3xLN	4607 \pm 131	186.1 \pm 4.92	146.5 \pm 3.63	92.8 \pm 3.42	239.3 \pm 3.18	362.8 \pm 3.42
Parity3xLG	5169 \pm 138	210.1 \pm 5.36	164.3 \pm 3.84	96.0 \pm 4.18	260.8 \pm 2.96	366.0 \pm 4.18
Parity3xHN	4471 \pm 155	198.3 \pm 6.06	144.9 \pm 4.30	85.5 \pm 6.54	262.2 \pm 3.56	366.9 \pm 4.76
Parity3xHG	5477 \pm 159	220.7 \pm 6.19	176.1 \pm 4.42	95.1 \pm 7.56	270.2 \pm 3.56	361.4 \pm 4.92
Calving year (CY)						
1994	4793 \pm 77	182.6 \pm 3.05	147.9 \pm 2.14	95.7 \pm 2.82	232.4 \pm 2.27	365.7 \pm 2.82
1995	4514 \pm 105	187.7 \pm 4.29	144.8 \pm 3.01	85.8 \pm 4.09	273.0 \pm 2.10	355.9 \pm 4.09
1996	4325 \pm 108	173.7 \pm 4.19	137.7 \pm 3.01	95.8 \pm 3.89	257.9 \pm 2.48	365.9 \pm 3.89
CY x T						
1994 x LN	4298 \pm 152	166.4 \pm 5.89	133.5 \pm 4.26	101.5 \pm 5.36	189.6 \pm 4.05	371.5 \pm 5.36
1994 x LG	4633 \pm 149	178.7 \pm 5.81	143.4 \pm 4.16	96.5 \pm 5.66	230.0 \pm 4.35	366.5 \pm 5.66
1994 x HN	4802 \pm 159	188.0 \pm 6.51	146.0 \pm 4.53	89.3 \pm 5.90	257.1 \pm 4.68	359.3 \pm 5.99
1994 x HG	5438 \pm 161	197.2 \pm 6.56	168.5 \pm 4.51	95.3 \pm 5.98	256.1 \pm 4.53	365.6 \pm 5.91
1995 x LN	4395 \pm 155	177.4 \pm 6.15	140.4 \pm 4.32	86.0 \pm 5.79	269.9 \pm 4.11	365.0 \pm 5.77
1995 x LG	4657 \pm 155	195.2 \pm 6.55	148.4 \pm 4.36	77.6 \pm 5.30	274.5 \pm 3.87	347.6 \pm 5.33
1995 x HN	4444 \pm 158	189.6 \pm 6.35	144.1 \pm 4.43	87.3 \pm 5.55	270.9 \pm 4.38	357.3 \pm 5.33
1995 x HG	4559 \pm 170	188.6 \pm 6.97	146.5 \pm 4.80	92.4 \pm 5.83	276.6 \pm 4.56	362.5 \pm 5.84
1996 x LN	4157 \pm 152	168.9 \pm 5.96	131.8 \pm 4.26	97.5 \pm 4.93	237.2 \pm 4.33	367.5 \pm 4.93
1996 x LG	5046 \pm 183	190.9 \pm 6.35	162.4 \pm 5.12	94.7 \pm 6.60	269.6 \pm 4.91	364.7 \pm 6.16
1996 x HN	3796 \pm 172	160.3 \pm 6.88	119.5 \pm 4.81	97.6 \pm 5.67	259.5 \pm 4.63	367.6 \pm 5.68
1996 x HG	4283 \pm 203	174.6 \pm 7.23	137.5 \pm 5.68	93.5 \pm 6.52	265.4 \pm 4.47	363.6 \pm 6.52

^aTreatment = LN (Low SR No Grain), LG (Low SR Grain), HN (High SR No Grain) and HG (High SR Grain)

^b Parity (Parities >2 were pooled and labelled Parity 3)

9.5 DISCUSSION

Cubic splines adequately fitted the test-day data in this study as demonstrated by the high correlation between observed and predicted milk yields, non-serial residuals, uncorrelated coefficients and lower percentage of estimated milk yields >35L. The low value of the Durbin-Watson statistics suggested the likely presence of positive auto-correlations between test-dates. This was expected given the fact that test-day milk yields are repeated measures on the same experimental unit with correlated responses (Jensen, 2001, Schaeffer, 2004). Druet *et al.* (2003) compared several functions in modeling the lactation curve of French Holstein using milk test-day records and reported that splines were more appealing because they adjusted the data well, were relatively insensitive to outliers, were flexible, and resulted in smooth curves without requiring the estimation of a large number of parameters. Semiparametric models such as splines are employed when the functional form of a covariate is unknown (Cantet *et al.* 2005). In this situation, the underlying smooth function is usually a nuisance parameter, and the interest lies in accounting for the effects of the regressor variable (Altman, 2000). To fit such a function, Eilers and Marx (1996) proposed penalized splines, a methodology that is closely connected to mixed models (Ruppert and Carroll 2000, Ruppert *et al.* 2003; Wand, 2003). Cantet *et al.* (2005) compared splines with other models and reported better goodness of fit for splines.

The adequacy of cubic splines in modelling test-day lactation data as reported in our study agrees with the previous reports by White *et al.* (1999), Silvestre *et al.* (2006) and Bohmanova *et al.* (2008). The initial, peak, and nadir daily milk yield reported in this study were similar to values obtained for pasture-based dairy cows (White *et al.* 1999, Garcia and Holmes, 2001), although the cows in this study exhibited greater post-peak milk yield persistency (Figure 9.1). Observed fat and protein yields recorded during mid-lactation are also consistent with the physiological downturn in fat yield following post peak milk decline, but also partially due to reduced body reserve mobilization and an increase in the partitioning of feed energy into body reserves as lactation progresses.

9.5.1 Effects of stocking rate and grain supplementation on the lactation curve.

The impact of high stocking rate did not affect initial milk and component yields (Figure 9.1 and Table 9.2). The higher persistency reported on high SR treatments can be partly attributed to higher pasture production and utilization especially during the summer and autumn, when pasture growth rate declined on the low SR treatments to 12 to 25 kgDM/ha/d compared to an average of 40 kgDM/ha/d produced on the higher SR treatments (Figure 9.1). The differences in initial and peak milk yields were not as pronounced during winter and spring when variation in pasture growth rate between both SR groups was low (3 - 7.5 kgDM/ha/d). The relatively lower initial and peak daily milk yields reported here compared to values reported by Horan *et al.* (2005), are attributable to the differences in both genetic merit and production systems between the two studies. They compared the performance of high genetic merit cows at both high SR and feeding systems in New Zealand while our studies did not focus on genetic merit and was conducted under the pasture-based system in Australia. Similarly, the higher persistency of milk yield in grain-supplemented treatments reported in this study is consistent with other reports of the effect of feeding high density energy diets compared with predominantly pasture-based diets (MacDonald 2008, Horan *et al.* 2005).

Results from studies in Australia and around the world had established that whole lactation response including the extra body weight and body condition gains and “carry-over” effect of extra pasture resulting from substitution should be considered when evaluating response to grain supplementation in dairy cows (Kellaway and Harrington 2004). Summarized reports (Kellaway and Harrington, 2004) of short-term experiments in Australia, measuring immediate responses to supplements over varying experimental periods averaged 0.5 - 0.80 kg milk/kg supplement, whereas response from long-term studies, including both immediate and residual responses, averaged 1.10 kg milk/kg supplement, which are similar to values reported in this study. Whole lactation response to grain supplementation in this study showed that the greatest response to grain feeding occurred when grain was used to improve productivity, weight gains, pasture consumption, and extend lactation length in LG and HG treatment groups. Similar results under stocking rate studies have been reported by Fike *et al.* (2003) and Tozer *et al.* (2004).

Feeding grain also helped to “buffer” the impact of adverse seasonal variations in pasture availability and quality. Grain supplementation in this study led to increased LL, (subject to seasonal variations), reduced DC and improved efficiency of feed conversion to MS in dairy cows grazing on both low and high SR. Penno *et al.* (1995) reported up to 40 days increase in LL, improved cow condition and pasture cover due to late season supplementation, but MacDonald *et al.* (2008) and Tozer *et al.* (2004), found no effect of SR on reproductive success and feed conversion efficiency, respectively.

9.5.2 Influence of environmental factors on lactation attributes

Reports on the influence of environment, production system, season and month of calving (Horan *et al.* 2005) also support the findings in this study. Under pasture-based systems, reduction in quantity and quality of pasture in the summer and autumn months in the Southern Hemisphere, depresses dry matter intake and milk yield. Terkeli *et al.* (2000) reported that month of calving and lactation stage influenced lactation while Horan *et al.* (2005) obtained significant influences of age at calving and DIM on milk yield. The coinciding of the physiological downturn in milk yield post-peak with periods of reduced pasture growth rates partly explains the increased performance of cows on the HN over the LN treatment (Figure 9.1). The improved pasture production from irrigation and high SR to utilize the extra pasture produced contributed to the observed responses and also emphasizes the need for efficient grazing and reproductive management under pasture-based systems.

9.5.3 Influence of curve shape on parity and reproduction

Lower peak yields and higher persistency in first compared with higher parity cows reported in this study agrees with the findings of Terkeli *et al.* (2000) and Horan *et al.* (2005). However, in contrast, first parity cows in this study attained peak yield 2-6 days later than higher parity cows, which may be a reflection of the treatments imposed. Increased rise to peak and total milk yield in higher parity cows compared with primiparous cows is attributable to the physiological effect of age on milk secretion rate and the combined effect of increase in body weight and udder development from repeated parturition (Mostert *et al.* 2001, Freeze and Richards 1992). Higher milk component yields associated with increasing parity, as found in this study, has also been

reported in the work of Freeze and Richards, (1992), although they found a declining protein yield with increasing parity.

High peak yields and steeper declines associated with longer CI and DC observed especially among cows on the LN treatment confirmed previous reports that high peaks and shaper post peak decline are physiologically stressful and could negatively impact on reproduction (Terkeli *et al.* 2000).

9.5.5 Effect of production level in early lactation on lactation attributes

High production in early lactation of high genetic merit or high producing cows have been reported in studies by Horan *et al.* (2005) and Fulkerson *et al.* (2001), although the influence of early lactation production level on the shape of the lactation curve has not been well studied. High correlation between production level and total milk yield found in this study suggests that this is an important management tool for dairy producers who are keen to identify early indicators of milk production potential in their cows. However, the relatively small number of observations (29 in the low production class compared with 93 and 94 for medium and high production classes, respectively) suggests the need for further studies on this criterion.

9.6 Conclusion

This study evaluated the usefulness of cubic splines in modelling lactation under pasture-based production systems and the use of a high stocking rate and grain supplementation to increase dairy productivity. The results demonstrate the usefulness of cubic splines as a smoothening function in lactation curve modelling, while simultaneously accounting for environmental factors affecting curve shapes, as evidenced by the high correlation between predicted and observed values and low residual variances. Using grain to maintain persistency for a longer time in mid-lactation is a good strategy for increasing per cow milk yield. Finally, cubic splines have been demonstrated to be very adequate in modelling daily milk yield in pasture-based production systems.

Chapter 10. General Conclusions and recommendations from the studies

This thesis examined the goodness of fits of many lactation functions to test-day milk and milk component data, determined the factors affecting the shape of lactation curves and evaluated the genetic parameters of lactation traits in pasture-based dairy systems.

Although the best overall models for fitting either herd or individual cow data based on goodness fit and simultaneous accounting for the effect of environmental factors on curve shapes were the polynomial and regression based models. However, the simpler empirical modes are easier to fit and they generate parameters that can be related to component of the lactation curve. Their main limitation is inability to simultaneously account for factors affecting each test-day. Until satisfactory meanings can be attributed to the parameters of the more complex models, the simpler ones will continue to be the model of choice in lactation curve studies.

Factors accounting for variation individual cow lactation curve shape have genetic and phenotypic components. This thesis contributed to the knowledge of lactation curve modelling and their suitability for dairy management decisions in Chapter 6 by evaluating the goodness of fit of empirical, mechanistic and semi-parametric models to lactation data from pasture-based dairy cows. The proposal of a *new empirical function* of lactation which compares favourably with four and five parameter models in goodness of fit to pasture-based data is *potentially valuable to research in lactation modelling*.

The studies also established the *typical dairy herd lactation pattern* of cows under the Tasmanian production system. This profile can be used to quickly identify variation in herd or individual cow yield patterns so that prompt identification of unexplained deviations from the pattern can be made. Variation in curves shapes due to herd, production year, season and parity indicate that there is scope to phenotypically improve lactation curve shape by targeting interventions such, appropriate season of calving and

grain supplementation to aspects of the management decisions. High positive correlations among parameters of the new LQ model with lactation persistency also indicate the possibility of genetic improvement by exploiting this attribute of the model.

Evaluation of ASI and APR influenced the rising phase of lactation but not peak milk yield which is known to be positively correlated with total milk yield. It is possible as was concluded in chapter five that using the APR as a basis for selecting breeding bulls will lead to better lifetime performance and more profitable milk yield rather than affecting the lactation curve shape. One of the useful findings of the thesis is the confirmation of an *early indicator of genetic merit* in milking dairy cows in the form of *milk yield potential during early lactation* i.e. average milk yield during the first 50-80 days in lactation which is highly positively correlated with total yield. This information derivable from test-day milk yields can be incorporated into breeding value estimation measures. However, coinciding of peak milk yield with, early lactation when there is high potential for milk energy imbalance, and re-breeding under pasture based systems, calls for effective supplementation strategy in order to mitigate the stress during early lactation.

The studies on stocking rate and pasture utilization support the hypothesis that pasture utilization is central to the economic viability of the pasture-based system but also highlighted the potential problem of irrigated pasture management under high stocking rate. Therefore training of producers on pasture management under irrigation will be an investment in the right direction. However using irrigation to increase pasture utilisation can potentially expose the industry to the risk of water stress and drought. It would be necessary for the industry to develop breeding programs for the identification of more robust and drought tolerant cows.

This study was not able to explore the occurrence of *atypical* lactations in pasture-based dairy cows. However trends in the occurrence of curve shapes (chapter 6 and 7) suggest that genetic and phenotypic as well as the mathematical properties of the function may be involved. Low fat:protein ratio in some of the data sets used in this study indicated the possibility of metabolic stress related milk component yield but further studies of the

relationship of curve shapes with the incidence of metabolic diseases could not be pursued further due to insufficient reliable records of metabolic diseases. This is an area of lactation curve modelling needing urgent answers.

A major limitation of empirical models is that their parameters cannot be related to known physiology of lactation in terms of the population and activity of secretory cells. Mechanistic models of lactation tend to fill this gap but evaluation of five mechanistic models to the available in this thesis failed to achieve high goodness of fit. Two options to consider are; further research into the potential of existing mechanistic models to fit data from a wide range of production systems and establishing a basis for understanding the physiological properties of empirical models. The newly proposed LQ model is simple and robust. Aspects of it needing further research are the estimation of lactation persistency from the parameters of the model and its application to understanding the underlying biology of lactation.

Incomplete records of animal pedigree at herd level hampered the estimation of breeding values in the various data utilised for this thesis. Accurate records facilitates more reliable breeding value estimation and enables producers to spot and deal with problems before they become too costly. Current lactation recording system in the study area is rather scanty in details on management practices. Approximation of herd practices as well as using monthly rather than weekly or daily test-day records can mask vital information. It is therefore of paramount importance to emphasise the inclusion of additional data on herd reproductive performance and the incidence of metabolic diseases on routing test-day data. Although not considered in this thesis, the inclusion of economic indices such as the price of milk and milk constituents, replacement animals and feed cost can improve the application of lactation curves for modelling profitability in dairy farms. The most productive cow is not necessarily the most profitable. This is an important future study area.

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